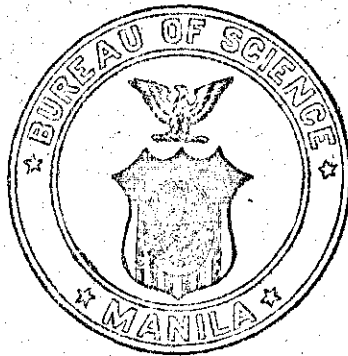


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THE RELATION OF SALT PROPORTIONS AND CONCENTRATIONS TO THE GROWTH OF YOUNG WHEAT PLANTS IN NUTRIENT SOLUTIONS CONTAINING A CHLORIDE¹

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TWELVE TEXT FIGURES

INTRODUCTION

For the development of higher plants the chemical elements carbon, hydrogen, oxygen, nitrogen, phosphorus, sulphur, calcium, magnesium, potassium, and iron are unquestionably necessary. Carbon mainly derived from the carbon dioxide of the air, together with hydrogen and oxygen, which enter through the roots in the form of water, make up by far the greater portion of the plant substance. But the other necessary elements must be supplied and they also enter through the roots from aqueous solution. With the exception of iron, of which but little is needed, these essential elements must be furnished in relatively large amounts.

That higher plants require nitrogen, sulphur, phosphorus, calcium, magnesium, potassium, and iron in an aqueous solution about their roots was pointed out very early by Birner and Lucanus.² These writers supplied the necessary elements in

¹ Botanical contribution from the Johns Hopkins University, No. 58.

² Birner, H., and Lucanus, B., Wasserculturversuche mit Hafer. (In der agr.-chem. Versuchs-station zu Regenwalde i. J. 1864 durchgeführt.) Landw. Versuchsst. 8 (1866) 128-177.

the form of the salts monopotassium phosphate, calcium nitrate, magnesium sulphate, and ferric phosphate. Oat plants grown in solutions that lacked any of these elements were found to have much smaller dry weights than those grown in the full nutrient solution. Similar experiments by later workers with many other kinds of higher plants have given the same general results; namely, that the dry yield is much greater when all seven of these elements are present in the culture solution than when one or more of them are omitted.

Birner and Lucanus also showed that these seven are the only elements that are necessary for excellent growth of oat plants. There has been considerable discussion, however, among various writers as to whether certain other elements may not be essential for plants in general or for certain plants in particular. Nobbe and others, for example, believed that chlorine was necessary for the complete development of the buckwheat plant.³ Beyer⁴ reported that the fruiting of oats and peas was not normal in culture solutions that lacked chlorine. Also, Salm-Horstmar⁵ was of the opinion that silicon and manganese were necessary for oats. But from all the work that has been done it may be concluded that for most higher plants only the seven elements mentioned above are to be regarded as essential constituents of the nutrient solution.

There still remains, however, the problem as to whether plant growth may not be significantly accelerated in the presence of nonessential elements, and modern investigators have studied the effects of a number of such elements. Of course it is well known that many unnecessary elements act as poisons and retard plant growth when supplied in certain concentrations, and the problem thus suggested has also been taken up by many writers.

³ Nobbe, F., and Siegert, T., Ueber das Chlor als specifischen Nahrstoff der Buchweizenpflanze, Landw. Versuchsst. 4 (1862) 318-340, and 5 (1863) 116-136; Beiträge zur Pflanzencultur in wässerigen Nahrstoff Lösungen. II. Ueber das Chlor als Pflanzennahrstoff, Landw. Versuchsst. 6 (1864) 108-120. Nobbe, F., Ueber die physiologische Function des Chlor in der Pflanze, Landw. Versuchsst. 7 (1865) 371-386. Leydhecker, A., Ueber die physiologische Bedeutung des Chlor in der Buchweizenpflanze, Landw. Versuchsst. 8 (1866) 177-187.

⁴ Beyer, A., Bericht über die im Sommer 1867 an der Versuchs-Station Regenwalde ausgeführten Wasserculturversuche, Landw. Versuchsst. 11 (1869) 262-287.

⁵ Salm-Horstmar, Vers. und Resultate üb. d. Nährung d. Pflanze. Braunschweig (1856).

Among the generally unessential elements that have been considered by investigators, chlorine is one of the commonest, and it has attracted considerable attention among agriculturists also. This element is frequently added to the soil as potassium chloride in fertilizer practice, and it has even been maintained that addition of sodium chloride to the soil results in an increased yield of certain crops. The present study deals with the influence of chlorine upon the growth of plants in a nutrient solution that also contains the seven essential elements.

Chlorine is not required in large amounts, since plants are able to grow and mature normally without appreciable amounts of this element. Birner and Lucanus (1886) concluded that chlorine was not essential; Knop,⁶ after growing many kinds of plants, including buckwheat, also concluded that chlorine was unnecessary for normal development. Wagner⁷ obtained apparently completely developed maize plants when no chlorine was in the culture solution. Recently Prianishnikov,⁸ employing both the water-culture and the sand-culture methods, was unable to establish the necessity of this element. Shulov⁹ concluded after several years of experimentation that chlorine is not necessary for the normal development of buckwheat plants.

Other investigators have found that many plants make very good growth without a chloride in the culture solution, and in no case has the necessity for the element chlorine been demonstrated. Crone,¹⁰ using a nutrient solution without chlorine, found that rape, barley, grape, and maize made excellent growth.

Shive¹¹ found that young wheat plants made better growth in a three-salt nutrient solution, containing the same salts as employed by Birner and Lucanus, than in any chloride-containing solution that he tested. Buckwheat also matured in Shive's

⁶ Knop, W., Quantitative Untersuchungen über den Ernährungsprozess der Pflanze, Landw. Versuchsst. 7 (1865) 93-107. Knop, W., and Dworzak, Ber. d. Sachs. Ges. d. Wiss. (1875) 61.

⁷ Wagner, P., Wassercultur-Versuche mit Mais. III. Vegetations-Versuche mit chlorfreier Lösung, Landw. Versuchsst. 13 (1871) 218-222.

⁸ Prianishnikov, D. N., Results of vegetation experiments in the years 1901-1903, Abstract in Exp. Sta. Rec. 18 (1906-1907) 320 and 321.

⁹ Shulov, L. S., Various smaller experiments with fertilizers and soils, Abstract in Exp. Sta. Rec. 22 (1910) 223.

¹⁰ Crone, G., Ergebnisse von Untersuchungen über die Wirkung der Phosphorsäure auf die höhere Pflanzen und eine neue Nährlösung, Sitzungsber. Niederrhein. Gesell. Natur- und Heilkunde, Bonn (1902) 167-173.

¹¹ Shive, J. W., A three-salt nutrient solution for plants, Am. Journ. Bot. 2 (1915) 157-160. A study of physiological balance in nutrient media, Physiol. Res. 1 (1916) 327-397.

three-salt solutions containing no chlorides. Apparently normal seeds were obtained repeatedly by Johnston from buckwheat plants grown in one of Shive's solutions, without any chloride.¹²

In spite of the fact that these experiments show that chlorine is not required in any considerable amount, it is probable that plants have never been grown without containing at least small amounts of chlorine. Most plants contain some chlorine and, besides typical saline plants, many contain relatively large amounts of chlorine in their ash.¹³ Since seeds probably always contain small amounts of this element, it cannot be regarded as actually proved that it is absolutely unnecessary. However, the fact that chlorine is found in the ash must not, of course, be considered proof that it is essential. Thus, sodium, silicon, aluminium, barium, strontium, manganese, zinc, arsenic, copper, boron, bromine, iodine, fluorine, cobalt, nickel, tin, and lead are all found in plant ash, and yet no experiments have shown that these are necessary to induce growth. But a very recent paper, of which I have seen only a brief review, appears to furnish evidence that very small amounts of chlorine are necessary for buckwheat. Pfeiffer and Simmermacher¹⁴ studied the significance of chlorine in fertilization experiments. Chlorine is reported as indispensable for the growth of buckwheat; but the amount of chlorine considered to be required was very small, and larger quantities of chlorine compounds were regarded as injurious.

As with many other nonessential elements, plants may be altered in their manner of growth by supplying them with chlorine, in addition to the small amount contained in the seed. Such alterations may result in accelerated or retarded growth, increase or decrease in yield, etc., and chlorides may therefore be

¹² Johnston, E. S., Seasonal variations in the growth-rates of buckwheat plants under greenhouse conditions, Johns Hopkins Univ. Circular (March, 1917) 211-217.

¹³ Hopkins, C. G., Soil Fertility and Permanent Agriculture. New York (1910) 603. Wolff, Emil, Aschen-Analysen von landwirtschaftlichen Producten, Fabrik-abfällen und wildwachsenden Pflanzen. I. Theil. Berlin (1871); Aschen-Analysen von land- und forstwirtschaftlichen Producten. II. Theil. Berlin (1880). Mangin, M. H., Sur la ficoideglaciale (*Mesembrianthemum crystallinum*), Compt. rend. Paris 96 (1883) 80-83.

¹⁴ Pfeiffer, Th., and Simmermacher, W., Landw. Versuchsst. 88 105-120. through Chem. Zentralbl. 1 (1916) 1186, and Chem. Abs. 11 (1917) 3365.

considered as beneficial or injurious, depending upon the desirability or undesirability of the changes produced by their use.

Tottingham¹⁵ presents a review of the literature on the effects of chlorides on plant growth, and reports experimental studies on the influence of chlorides on the growth of a number of agricultural plants. He reports that the introduction of potassium and sodium chlorides into solution cultures had little effect on wheat seedlings. Both yield of dry matter and length of roots were depressed in buckwheat grown to maturity in similar cultures. In soil cultures, radish was affected only slightly by chlorides; increased production of dry matter and sugar content resulted with carrot, while the reverse was true of parsnip. Sugar beet, in soil cultures, produced more watery roots and a greater amount of dry matter; the roots contained more glucose, but less sucrose. Similar responses followed the application of common salt alone to beets grown in the field. The potato produced increased yields of dry matter in the tuber when potassium chloride was supplied in place of potassium sulphate, in a complete fertilizer ration, to soil cultures in the greenhouse. Different varieties responded differently according to the percentage of starch. In field cultures in a dry season the application of potassium chloride in a complete fertilizer decreased the yield of dry matter in the tubers, but not the percentage of marketable tubers, of the Triumph variety. In a season that was very humid toward its close, no significant differences in composition or cooking qualities were found between tubers of the Rural New Yorker variety produced, when potassium sulphate and potassium chloride were employed separately in a complete fertilizer ration. Sodium chloride applied alone altered the composition of the tubers only slightly, but affected their quality seriously. It has, of course, been found that growth may be retarded when chlorides are supplied in very large amounts.¹⁶

¹⁵ Tottingham, W. E., A preliminary study of the influence of chlorides upon the growth of certain agricultural plants, *Journ. Am. Soc. Agron.* 11 (1919) 1-32.

¹⁶ Wheeler, H. J., and Hartwell, B. J., Conditions determining the poisonous action of chlorides, *Rhode Island Exp. Sta. Ann. Rep.* 15 (1901-1902) 287-304.

Increased growth is reported to have followed the application of sodium chloride to the soil, especially in the case of experiments carried out in the British Isles.¹⁷ From the point of view of physiology it is of course possible that under certain conditions the addition of chlorides to a nutrient solution may produce increased growth, as has been found for many salts of proved toxic action.¹⁸

Not only alterations in the amount of substance produced but also changes in the structure and physiological nature of plants have been brought about by the addition of chlorides to the nutrient medium.¹⁹ Harter²⁰ found that the addition of sodium chloride to the soil of experimental cultures might either increase or decrease the transpiration rate, and alter the structure of wheat, oat, and barley plants.

It is possible that chlorides may affect certain special metabolic processes and thus influence the plant more in one stage of its development than in another. Nobbe and his coworkers reported that chlorides were beneficial for the production of seed by buckwheat plants. He considered that this result was due to an influence exerted by chlorine upon the translocation of carbohydrate food; but Nobbe's observations have not been substantiated by more recent research.

It seems to be well established that many kinds of plants may be grown successfully in liquid media without any chloride. Nevertheless, most of the culture solutions recommended in the literature of plant physiology include a chloride. The following solutions may be mentioned as belonging to this class:

¹⁷ Dyer, B., Field experiments on cabbages at Rusper, Horsham, Journ. Roy. Agric. Soc. England, II 23 (1887) 425-430. Gonehalli, V. H., Common salt and its use as manure in the Konkan Division, Dept. Agric. Bombay Bull. 29, 19 pp. 1914. Voelcker, G. A., Experiments on the use of salt for mangolds, Journ. Roy. Agric. Soc. England 69 (1908) 355-366. Griffiths, A. B., A treatise on Manure, or the Philosophy of Manuring. London (1889) 399 pp.

¹⁸ Brenchley, W. E., Inorganic Plant Poisons and Stimulants. Cambridge (1914) 110 pp.

¹⁹ Hansteen, B., Ueber das Verhalten der Kulturpflanzen zu den Bodensalzen, I. and II. Jahrb. f. wiss. Bot. 47 (1910) 289-376.

²⁰ Harter, L. L., The influence of a mixture of soluble salts, principally sodium chloride, upon the leaf structure and transpiration of wheat, oats, and barley, Bull. U. S. Dept. Agric. Bur. Pl. Ind. 134 (1908) 22 pp.

Sachs:²¹ NaCl, CaSO₄, MgSO₄, Ca₃(PO₄)₂, KNO₃.
 Nobbe:²² KCl, MgSO₄, KH₂PO₄, Ca(NO₃)₂.
 Tollens:²³ NaCl, MgSO₄, KH₂PO₄, KNO₃, Ca(NO₃)₂.
 Schimper:²⁴ NaCl, MgSO₄, K₂HPO₄, KNO₃, Ca(NO₃)₂.
 Detmer:²⁵ KCl, MgSO₄, KH₂PO₄, Ca(NO₃)₂.
 Pfeffer:²⁶ KCl, MgSO₄, KH₂PO₄, KNO₃, Ca(NO₃)₂.
 Hartwell, Wheeler, and Pember:²⁷ KCl, MgSO₄, Ca(NO₃)₂,
 Ca(H₂PO₄)₂.

Stiles:²⁸ NaCl, MgSO₄, KH₂PO₄, KNO₃, CaSO₄.

Brenchley:²⁹ NaCl, MgSO₄, KH₂PO₄, KNO₃, CaSO₄.

On the other hand, very few nutrient solutions without a chloride have been recommended for plant cultures. Of this smaller group the following are familiar examples:

Knop (Tottingham):³⁰ MgSO₄, KH₂PO₄, KNO₃, Ca(NO₃)₂.

²¹ Sachs, J., Bericht über die physiologische Thätigkeit an der Versuchstation in Tharandt. IV. Vegetations-Versuche mit Ausschluss des Bodens über die Nährstoffe und sonstigen Ernährungsbedingungen von Mais, Bohnen und anderen Pflanzen, Landw. Versuchsst. 2 (1860) 219-268.

²² Nobbe, F., Ueber die physiologische Function des Chlor in der Pflanze, Landw. Versuchsst. 7 (1865) 371-386.

²³ Tollens, B., Ueber einige Erleichterungen bei der Cultur von Pflanzen in wässerigen Lösungen, Journ. Landw. 30 (1882) 537-540.

²⁴ Schimper, A. F. W., Zur Frage der Assimilation der Mineralsalze durch die grüne Pflanze, Flora 73 (1890) 207-261.

²⁵ Detmer, W., Practical plant physiology. Translated by S. A. Moor. London (1898) 2.

²⁶ Pfeffer, W., The physiology of plants. Translated by A. J. Ewart. Oxford 1 (1900) 420.

²⁷ Hartwell, B. F.; Wheeler, H. J.; and Pember, F. R.; The effect of the addition of sodium to deficient amounts of potassium upon the growth of plants in both water and sand cultures, Rhode Island Agric. Exp. Sta. Ann. Rep. 20 (1907) 299-357.

²⁸ Stiles, W., On the relation between the concentration of the nutrient solution and the rate of growth of plants in water culture, Ann. Bot. 29 (1915) 89-96.

²⁹ Brenchley, W. E., The effect of the concentration of the nutrient solution on the growth of barley and wheat in water cultures, Ann. Bot. 30 (1916) 77-90.

³⁰ Knop, W., Quantitativ-analytische Arbeiten über den Ernährungsprocess der Pflanzen. II. Landw. Versuchsst. 4 (1862) 173-187. Tottingham, W. E., A quantitative chemical and physiological study of nutrient solutions for plant cultures, Physiol. Res. 1 (1914) 133-245.

Birner and Lucanus (Shive):³¹ MgSO_4 , KH_2PO_4 , $\text{Ca}(\text{NO}_3)_2$.
Crone:³² CaSO_4 , MgSO_4 , $\text{Ca}_3(\text{PO}_4)_2$, KNO_3 .

The study to be reported in the present paper was undertaken, as has been stated, to throw more light upon the problem as to what may be the physiological influence upon plants of considerable amounts of potassium chloride in a nutrient solution that also contains other salts supplying all the essential elements.

This investigation was carried out at the Laboratory of Plant Physiology of the Johns Hopkins University, under the direction of Prof. B. E. Livingston, to whom I am indebted for valuable assistance during its progress and for aid in the preparation of this paper. I am also indebted to Dr. H. E. Pulling for many suggestions.

GENERAL METHODS

The experimental work comprised four series of cultures carried out at different times. The first two of these were planned to furnish a general survey of the relations between plant growth and salt proportions with a single total concentration of the solution (osmotic value 1.60 atmospheres). The results obtained from these two series made it appear desirable to test the effects of higher partial concentrations of potassium chloride than had been originally planned, and the third series included such tests. Finally, the influence of the total concentration of the medium was studied for four selected sets of salt proportions; these tests made up the fourth series. The present section will begin with an account of the general methods employed in all four series. This will be followed by a more detailed account of the methods employed, the results obtained, and a discussion of these results for each of the series taken in order.

In the nutrient solutions of the present study the essential elements (besides iron) were supplied as monopotassium phosphate, calcium nitrate, and magnesium sulphate, and the chloride ion was added by the introduction of potassium chloride.

³¹ Birner, H., and Lucanus, B., Wasserculturversuche mit Hafer. (In der agr.-chem. Versuchsstation zu Regenwalde i. J. 1864 durchgeführt.) Landw. Versuchsst. 8 (1866) 128-177. Shive, J. W., A study of physiological balance in nutrient media, *Physiol. Res.* 1 (1915) 327-397.

³² Crone, G., Ergebnisse von Untersuchungen über die Wirkung der Phosphorsäure auf die höhere Pflanzen und eine neue Nährlösung. Sitzungsber. Niederrhein. Nat.- und Heilkunde. Bonn. (1902) 167-173.

Thus the solutions here considered are four-salt solutions, and they are similar in their general make-up to the other four-salt solutions already employed by Tottingham. It will be seen that a solution made up of monopotassium phosphate, calcium nitrate, magnesium sulphate, and potassium chloride may be derived from the proper one of Shive's three-salt series by the addition of potassium chloride. These four salts have been employed in Nobbe's solution in a single set of proportions and in the so-called Detmer's solution in another set of proportions, as pointed out above. The present study aimed primarily to employ these four salts in various proportions, the total concentration of the solution remaining the same. The effects of different total concentrations with a constant set of salt proportions was also studied to some extent.

Culture solutions.—The culture solutions, whose compositions are given among the other data of the individual experiments, were prepared from analyzed chemicals³³ and water obtained from a "Barnstead" still. Each salt was dissolved separately, and the exact concentration of the resulting solution was determined by chemical analysis (except in the case of potassium chloride). This procedure is especially necessary for solutions of calcium nitrate and of magnesium sulphate, because these salts contain amounts of water of crystallization that vary between wide limits, and because they are rather readily decomposed by heat. Upon dilution to convenient volume-molecular concentrations,³⁴ these solutions became the "stock solutions" from which the various culture media were prepared. The stock solutions were stored (never longer than one month) in cork-stoppered glass bottles.

Ferric phosphate (used as a source of iron) was prepared from a ferric nitrate solution by precipitation with a one-fourth molecular solution of monopotassium phosphate. The precipitate was obtained in a finely divided condition by using cold solutions and by constantly stirring while the potassium salt was added. After thoroughly washing the precipitate, it was shaken with sufficient water to form a suspension containing approximately 0.0022 gram of ferric phosphate, or 0.0008 gram of iron, in each cubic centimeter.

³³ The potassium chloride was the Baker and Adamson Chemical Company's "analyzed" salt; the other salts were the J. T. Baker Chemical Company's "analyzed" salts.

³⁴ By volume-molecular concentration is meant the number of gram molecules contained in each liter of solution.

For the preparation of the culture solutions, the required amount of each stock solution was drawn from a burette into a volumetric flask partially filled with distilled water, and the flask was finally filled to the mark with more water. For the cultures in series IV, in which culture solutions ranging from 0.50 to 7.00 atmospheres were employed, stock culture solutions of 7.00 atmospheres were prepared and the less-concentrated culture solutions were made by proper dilution. The culture solutions were poured from the volumetric flasks into the culture jars, and two drops of the suspension of ferric phosphate were added to each complete solution. The culture jars were wide-mouthed glass bottles of 250 cubic centimeters capacity, which had been used for several years in similar experiments.

The plants.—The wheat seeds used in these studies were supplied by the Bureau of Plant Industry of the United States Department of Agriculture. The variety was "Fulcaster," C. I. No. 1918, grown at the Arlington Experiment Farm, Arlington, Va., in 1915. The seeds were germinated in moist chambers and then transferred to a netting germinator. At the end of about five days, when the seedlings were from 8 to 10 centimeters high, they were transferred from the germinator to the culture solutions.

The internal differences between seedlings grown from the same stock of seed and exposed to practically identical external conditions constitute a source of great difficulty in work with water-cultures.³⁵ To minimize such variations, seedlings were selected that were as nearly alike as possible, this selection being made on the basis of the appearance of the seedlings. Two selections were made, the first when the sprouted seeds were transferred to the netting germinators, and the second when the plants were transferred to the culture jars.

Six seedlings were used in each culture. These were supported by cotton in holes near the margin of the cork, the seed remnants remaining below the cork. To prevent entrance of light to the roots, the jars were covered with cardboard covers.

The method of supporting the stem and leaves is important, because the rate of transpiration, and probably that of photosyn-

³⁵ This has been emphasized by Stiles. Stiles, W., On the relation between the concentration of the nutrient solution and the rate of growth of plants in water culture, *Ann. Bot.* 29 (1915) 89-96. Observations on the influence of aeration of the nutrient solution in water culture experiments, with some remarks on the water culture method, *New Phytol.* 16 (1917) 181-197.

thesis and other processes, may be greatly modified by the way in which the leaves are exposed to the air. The pointed end of a cylindrical wooden rod (a quarter-inch dowel), 6 millimeters in diameter and 30 centimeters long, was set into a hole in the center of the cork. A loop (5 centimeters in diameter) of paraffined copper wire, the lower part of which was wrapped around the rod several times, was used to hold the plant erect.⁸⁶ As the height of the plants increased, the loop was raised on the rod. Care was taken to support all the plants in the same way.

The same aërial conditions were secured for all the cultures in a series by rotating the cultures near the margins of the circular tables described by Shive. Each of the cultures was thus exposed to approximately the same changes in light, temperature, and humidity conditions.

The frequency with which the culture solutions are renewed is very important in experiments with solution cultures.⁸⁷ The solutions here used were changed every four days. Thus the period between changing is not strictly comparable with that used by Shive and by Tottingham, each of whom employed a three-day period. When the solutions were changed the decrease in volume of the solution during the previous period was measured, and the amount of solution found to have been removed was taken as an approximate measure of the amount of water absorbed and transpired during the period.

The developmental stage of the plants probably has an important bearing on their salt requirements.⁸⁸ The present study is concerned only with the early vegetative stage of the young wheat plants. When transferred from the germinators to the

⁸⁶ For photograph see McCall, A. G., A new method for the study of plant nutrients in sand cultures, *Journ. Amer. Soc. Agron.* 7 (1915) 250-252.

⁸⁷ Trelease, S. F., and Free, E. E., The effect of renewal of the culture solutions on the growth of young wheat plants in water-cultures, *Johns Hopkins Univ. Circ. N. S. No. 3* (March, 1917) 227 and 228. Merrill, M. C., Some relations of plants to distilled water and certain dilute toxic substances, *Ann. Missouri Bot. Gard.* 2 (1915) 459-606. Stiles, W., On the interpretation of the results of water culture experiments, *Ann. Bot.* 30 (1916) 427-436. Brenchley, W. E., The effect of the concentration of the nutrient solution on the growth of barley and wheat in water cultures, *Ann. Bot.* 30 (1916) 77-90.

⁸⁸ Pember, F. R., Studies by means of both pot and solution cultures of the phosphorous and potassium requirements of the barley plant during its different periods of growth, *Bull. Agric. Exp. Sta. Rhode Island State College* 169 (1917) 1-50.

culture solutions the plants were about five days old. They were grown in the culture solutions, renewed every four days, for twenty-four days, except in the case of series III and IV in which the growth period was extended to thirty-two days.

At the end of the growth period the plants were harvested for the determination of their dry weight. Notes were made at this time of the appearance of the tops and roots, special attention being given to apparent pathological conditions that might indicate injury from unbalanced salt nutrition. The tops and roots were harvested separately, the roots being severed from the tops at the point of attachment of the seed.³⁹ The tops and roots were dried separately for about two days, at a temperature of 102–105° C., to approximately constant weight, and the dry weights were then determined.

The experiments were conducted in one of the greenhouse rooms of the Laboratory of Plant Physiology, on the outskirts of the city of Baltimore. The evaporating power of the air for the period of each experiment was determined by means of Livingston white spherical porous-cup atmometers,⁴⁰ one of the instruments being operated on each of the rotating tables. The atmometer bottle was placed 10 centimeters from the center of the table, the top of the sphere being 40 centimeters above the table top. The atmometers were read every four days, when the solutions were changed. A record of fluctuations in temperature was obtained by means of a Richard thermograph placed in the shade near the plants.

SERIES I

METHODS OF SERIES I

Series I was continued for twenty-four days, from January 11 to February 4, 1916. During this period the highest air temperature was 29° C., on January 26, and the lowest was 10° C., on January 17. The average daily maximum temperature for the period was 25° C., and the average daily minimum 18° C. The mean daily water loss from a white spherical porous-cup atmometer, indicating the evaporating power of the air, was 17.2

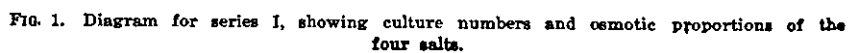
³⁹ The seed-coat remnants were dried and weighed with the roots; Shive discarded them.

⁴⁰ Livingston, B. E., *Atmometry and the porous cup atmometer*, *Plant World* 18 (1915) 21–30, 51–74, 95–111, 143–149. Also reprinted, Tucson, Ariz. (1915).

cubic centimeters, and the total loss for the entire period was 415 centimeters.

The general plan of this series is similar to that employed by Tottingham. Eighty-four solutions were made from four salts: potassium chloride, monopotassium phosphate, calcium nitrate, and magnesium sulphate. In each solution the four salts were so proportioned that the total concentration of each solution corresponded to 1.6 atmospheres of osmotic pressure at 25° C., and in the different solutions the proportion of each salt was varied by 0.1 of the total osmotic concentration of all salts. The lowest concentration of any salt was thus 0.1 of the total concentration and the greatest 0.7. All of the possible different proportions were used that could be produced by these variations. Thus, there were eighty-four different solutions in this series, all of which had approximately the same total osmotic concentration, but no two of which had the same set of salt proportions. This may be stated in another way by saying that all of the solutions were planned to have the same total number of particles (ions plus molecules) per unit volume, but no two solutions the same proportions of the different kinds of particles. Besides the eighty-four solutions belonging in the series, Shive's best three-salt solution for wheat and Tottingham's best four-salt solution for wheat were employed for the sake of comparison.

If three salts had been employed instead of four, the compositions of the solutions could have been represented graphically by means of points placed in an equilateral triangle, the points being so placed that the least concentration of one salt would have been along one side of the triangle and the greatest at the opposite angle. As four salts were used, a figure representing their various proportions assumes the form of a regular tetrahedron. In this figure each face of the tetrahedron represents 0.1 concentration of one salt and the opposite apex 0.7. Since seven proportions of each salt were employed, different concentrations of the salt whose lowest concentration is represented by the base of the figure will fall in seven planes. For convenience of graphical presentation the planes representing the different concentrations of potassium chloride have been plotted separately (fig. 1). Since only one culture that had the greatest concentration of potassium chloride was used, the plane which passes through the apex is represented by a point; the



other planes are represented by triangles. The seven triangles in fig. 1 (numbered T1 to T7) represent as many horizontal planes passed through the tetrahedron and all the points upon any one triangle denote solutions having the same partial concentration of potassium chloride. Similarly, the position of a point upon any one of the triangles indicates the osmotic proportions of the other three salts in the corresponding solution. The lines are so drawn that their intersections represent the salt proportions actually employed. It will be seen that there are twenty-eight solutions (triangle 1) that are characterized by having 0.1 of their total osmotic concentration due to potassium chloride, while there is but one solution (triangle 7) in which 0.7 is due to this salt.⁴¹ Each solution will be designated by a triple number, the first part denoting the triangle (as T2), the second the horizontal row of intersections in that triangle (as R3), and the third representing the number of the intersection in the row, counted from left to right (as C2). The solution just described is thus named T2R3C2, and the four salts contribute, respectively, the following proportions of the total concentration: potassium chloride, 0.2; monopotassium phosphate, 0.3; calcium nitrate, 0.2; and magnesium sulphate, 0.3. The triangle number gives the number of tenths due to potassium chloride, the row number gives the number of tenths due to monopotassium phosphate, and the culture number gives the number of tenths due to calcium nitrate. The number of tenths of the total concentration due to the fourth salt (magnesium sulphate) is found by subtracting from 10 the sum of the numbers appearing in the designation of the solution.

The actual chemical composition of each of the eighty-four solutions in series I is given in Table 1, in terms of the volume-molecular partial concentrations of the four salts. The first column of this table gives the culture numbers of the solutions just described, and the last three columns give the three cation-ratio values of each solution, which will be referred to later. To obtain these concentration values, it was necessary to calculate the volume-molecular partial concentrations of each salt that would produce 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, and 0.7 of 1.60 atmospheres of osmotic pressure at 25° C. The values thus obtained are given in Table 2.

⁴¹ For a more detailed discussion of the interpretation of this kind of diagram, Tottingham's paper may be referred to.

TABLE 1.—Partial concentrations of potassium chloride, monopotassium phosphate, calcium nitrate, and magnesium sulphate in each of the solutions employed in series I; also the values of the three cation ratios; total osmotic value of each solution, 1.60 atmospheres.

Culture No.	Volume-molecular concentration.				Cation-ratio value.		
	KCl.	KH ₂ PO ₄ .	Ca (NO ₃) ₂ .	MgSO ₄ .	Mg/Ca.	Mg/K.	Ca/K.
	<i>M.</i>	<i>M.</i>	<i>M.</i>	<i>M.</i>			
T1R1C1.....	0.0033	0.0033	0.0023	0.0309	13.43	4.68	0.25
C2.....	0.0033	0.0033	0.0047	0.0261	5.55	3.95	0.71
C3.....	0.0033	0.0033	0.0072	0.0216	3.00	3.27	1.09
C4.....	0.0033	0.0033	0.0098	0.0171	1.75	2.59	1.48
C5.....	0.0033	0.0033	0.0124	0.0126	1.02	1.91	1.88
C6.....	0.0033	0.0033	0.0150	0.0081	0.54	1.23	2.27
C7.....	0.0033	0.0033	0.0177	0.0038	0.21	0.58	2.68
R2C1.....	0.0033	0.0068	0.0023	0.0261	11.35	2.58	0.23
C2.....	0.0033	0.0068	0.0047	0.0216	4.60	2.14	0.47
C3.....	0.0033	0.0068	0.0072	0.0171	2.38	1.69	0.71
C4.....	0.0033	0.0068	0.0098	0.0126	1.29	1.25	0.97
C5.....	0.0033	0.0068	0.0124	0.0081	0.65	0.80	1.23
C6.....	0.0033	0.0068	0.0150	0.0038	0.25	0.38	1.49
R3C1.....	0.0033	0.0103	0.0023	0.0216	9.39	1.59	0.17
C2.....	0.0033	0.0103	0.0047	0.0171	3.64	1.26	0.35
C3.....	0.0033	0.0103	0.0072	0.0126	1.75	0.93	0.53
C4.....	0.0033	0.0103	0.0098	0.0081	0.83	0.60	0.72
C5.....	0.0033	0.0103	0.0124	0.0038	0.31	0.28	0.91
R4C1.....	0.0033	0.0138	0.0023	0.0171	7.44	1.00	0.13
C2.....	0.0033	0.0138	0.0047	0.0126	2.68	0.74	0.27
C3.....	0.0033	0.0138	0.0072	0.0081	1.13	0.47	0.42
C4.....	0.0033	0.0138	0.0098	0.0038	0.39	0.22	0.57
R5C1.....	0.0033	0.0173	0.0023	0.0126	5.48	0.61	0.11
C2.....	0.0033	0.0173	0.0047	0.0081	1.72	0.39	0.23
C3.....	0.0033	0.0173	0.0072	0.0038	0.53	0.18	0.85
R6C1.....	0.0033	0.0208	0.0023	0.0081	3.52	0.84	0.10
C2.....	0.0033	0.0208	0.0047	0.0038	0.81	0.16	0.20
R7C1.....	0.0033	0.0243	0.0023	0.0038	1.65	0.14	0.08
T2R1C1.....	0.0067	0.0033	0.0023	0.0261	11.35	2.61	0.23
C2.....	0.0067	0.0033	0.0047	0.0216	4.60	2.16	0.47
C3.....	0.0067	0.0033	0.0072	0.0171	2.38	1.71	0.73
C4.....	0.0067	0.0033	0.0098	0.0126	1.29	1.26	0.99
C5.....	0.0067	0.0033	0.0124	0.0081	0.65	0.81	1.24
C6.....	0.0067	0.0033	0.0150	0.0038	0.25	0.38	1.50
R2C1.....	0.0067	0.0068	0.0023	0.0216	9.39	1.60	0.17
C2.....	0.0067	0.0068	0.0047	0.0171	3.64	1.27	0.35
C3.....	0.0067	0.0068	0.0072	0.0126	1.75	0.93	0.53
C4.....	0.0067	0.0068	0.0098	0.0081	0.83	0.60	0.73
C5.....	0.0067	0.0068	0.0124	0.0038	0.31	0.28	0.92
R3C1.....	0.0067	0.0103	0.0023	0.0171	7.44	1.01	0.14
C2.....	0.0067	0.0103	0.0047	0.0126	2.68	0.74	0.28
C3.....	0.0067	0.0103	0.0072	0.0081	1.13	0.48	0.42
C4.....	0.0067	0.0103	0.0098	0.0038	0.39	0.22	0.58

TABLE 1.—Partial concentrations of potassium chloride, monopotassium phosphate, calcium nitrate, and magnesium sulphate in each of the solutions employed in series I; also the values of the three cation ratios; total osmotic value of each solution, 1.6 atmospheres—Continued.

Culture No.	Volume-molecular concentration.				Cation-ratio value.		
	KCl.	KH ₂ PO ₄ .	Ca. (NO ₃) ₂	MgSO ₄ .	Mg/Ca.	Mg/K.	Ca/K.
	M.	M.	M.	M.			
T2R4C1.....	0.0067	0.0138	0.0023	0.0126	5.48	0.61	0.11
C2.....	0.0067	0.0138	0.0047	0.0081	1.72	0.40	0.23
C3.....	0.0067	0.0138	0.0072	0.0038	0.53	0.19	0.35
R5C1.....	0.0067	0.0173	0.0023	0.0081	3.52	0.34	0.10
C2.....	0.0067	0.0173	0.0047	0.0038	0.81	0.16	0.20
R6C1.....	0.0067	0.0208	0.0023	0.0038	1.65	0.14	0.08
T3R1C1.....	0.0101	0.0033	0.0023	0.0216	9.39	1.61	0.17
C2.....	0.0101	0.0033	0.0047	0.0171	3.64	1.28	0.35
C3.....	0.0101	0.0033	0.0072	0.0126	1.75	0.94	0.54
C4.....	0.0101	0.0033	0.0098	0.0081	0.83	0.60	0.73
C5.....	0.0101	0.0033	0.0124	0.0038	0.31	0.28	0.93
R2C1.....	0.0101	0.0068	0.0023	0.0171	7.44	1.01	0.14
C2.....	0.0101	0.0068	0.0047	0.0126	2.68	0.75	0.23
C3.....	0.0101	0.0068	0.0072	0.0081	1.13	0.48	0.43
C4.....	0.0101	0.0068	0.0098	0.0038	0.39	0.22	0.58
R3C1.....	0.0101	0.0103	0.0023	0.0126	5.48	0.62	0.11
C2.....	0.0101	0.0103	0.0047	0.0081	1.72	0.40	0.23
C3.....	0.0101	0.0103	0.0072	0.0038	0.53	0.19	0.35
R4C1.....	0.0101	0.0138	0.0023	0.0081	3.52	0.34	0.10
C2.....	0.0101	0.0138	0.0047	0.0038	0.81	0.16	0.20
R5C1.....	0.0101	0.0173	0.0023	0.0038	1.65	0.14	0.08
T4R1C1.....	0.0135	0.0033	0.0023	0.0171	7.44	1.02	0.14
C2.....	0.0135	0.0033	0.0047	0.0126	2.68	0.75	0.23
C3.....	0.0135	0.0033	0.0072	0.0081	1.13	0.48	0.43
C4.....	0.0135	0.0033	0.0098	0.0038	0.39	0.23	0.58
R2C1.....	0.0135	0.0068	0.0023	0.0126	5.48	0.62	0.11
C2.....	0.0135	0.0068	0.0047	0.0081	1.72	0.40	0.23
C3.....	0.0135	0.0068	0.0072	0.0038	0.53	0.19	0.35
R3C1.....	0.0135	0.0103	0.0023	0.0081	3.52	0.34	0.10
C2.....	0.0135	0.0103	0.0047	0.0038	0.81	0.16	0.20
R4C1.....	0.0135	0.0138	0.0023	0.0038	1.65	0.14	0.08
T5R1C1.....	0.0170	0.0033	0.0023	0.0126	5.48	0.62	0.11
C2.....	0.0170	0.0033	0.0047	0.0081	1.72	0.40	0.23
C3.....	0.0170	0.0033	0.0072	0.0038	0.53	0.19	0.35
R2C1.....	0.0170	0.0068	0.0023	0.0081	3.52	0.34	0.10
C2.....	0.0070	0.0068	0.0047	0.0038	0.81	0.16	0.20
R3C1.....	0.0170	0.0103	0.0023	0.0038	1.65	0.14	0.08
T6R1C1.....	0.0205	0.0033	0.0023	0.0081	3.52	0.34	0.10
C2.....	0.0205	0.0033	0.0047	0.0038	0.81	0.16	0.20
R2C1.....	0.0205	0.0068	0.0023	0.0038	1.65	0.14	0.08
T7R1C1.....	0.0240	0.0033	0.0023	0.0038	1.65	0.14	0.08

TABLE 2.—Partial concentrations of each of the four salts required to produce from 0.1 to 0.7 of the total osmotic concentration of 1.60 atmospheres for series I.

Fractional parts of 1.60 atmospheres.	KCl.	KH ₂ PO ₄ .	Ca(NO ₃) ₂ .	MgSO ₄ .
	<i>M.</i>	<i>M.</i>	<i>M.</i>	<i>M.</i>
0.1	0.0033	0.0038	0.0023	0.0038
0.2	0.0067	0.0068	0.0047	0.0081
0.3	0.0101	0.0108	0.0072	0.0126
0.4	0.0135	0.0138	0.0098	0.0171
0.5	0.0170	0.0173	0.0124	0.0216
0.6	0.0205	0.0208	0.0150	0.0261
0.7	0.0240	0.0243	0.0177	0.0309

The method used in these calculations may be illustrated with potassium chloride, the calculations for the other salts being made in the same way. It was first necessary to obtain certain physico-chemical data regarding each of the four salts dealt with, and these data as used for potassium chloride are given in Table 3. The numbers in the first column represent the tenths (from 0.1 to 0.7) of the total concentration of 1.60 atmospheres. Those in the second column represent the corresponding actual pressures in atmospheres. According to the van't Hoff equation, $\pi = CRT$, the osmotic value (π) of any solution may be obtained from the concentration of the particles in solution (C), the gas constant (R), and the absolute temperature (T).⁴² If the osmotic value is expressed in atmospheres, then R has the value 0.08207. The osmotic values here used are all calculated for a temperature of 25° C. (298° Abs.), so that T becomes 298, and the equation may be restated:

$$\pi = (298) (0.08207) C = 24.46 C.$$

For substances which do not dissociate or polymerize or form hydrates in solution the concentration, C , corresponds to the volume-molecular concentration, M ; and the osmotic pressure formula becomes: $\pi = 24.46 M$. But for salts, such as potassium chloride, which dissociate in solution into ions, $C = iM$;

⁴² The osmotic pressure equation here used must be understood to be only approximately true for solutions such as are dealt with in the present work. It really applies only to very *dilute solutions*. For a good discussion of osmotic pressure equations see Washburn, E. W., *Principles of Physical Chemistry*. New York (1915) 150-164. Also see Renner, O., *Ueber die Berechnung des osmotischen Druckes*, *Biol. Centralbl.* 32 (1912) 486-504.

in this equation i is the van't Hoff coefficient (or "mole-number"), which may be defined as the quotient of the number of particles actually present in the solution, divided by the number that would be present in an equal volume-molecular concentration of a substance that is unmodified in solution. Consequently, for salts the osmotic pressure formula becomes: $\pi = 24.46 \ iM$. For un-ionized substances i is unity, and for ionized substances such as salts i has a value greater than unity. The equation may be written in the form:

$$iM = \frac{\pi}{24.46}$$

By substituting for π in this equation each of the partial osmotic pressures from the second column of Table 3, the corresponding values of iM were obtained, and these are given in the fourth column. They represent the osmotic concentrations which are necessary to give the corresponding partial osmotic pressures given in the second column.

TABLE 3.—Data used in calculating the partial concentrations (column III) of potassium chloride required to give from 0.1 to 0.7 of the total osmotic concentration of 1.60 atmospheres, for series I.

I. Fractional parts of total con- centration (1.60 atmo- spheres).	II. Partial os- motic pres- sures.	III. Volume- molecular concentra- tion of KCl.	IV. Degree of ionization.	V. "Mole- number," or van't Hoff coef- ficient, i .	VI. Concentra- tion calcu- lated from $C=iM$.
	<i>Atm.</i>	<i>M.</i>			
		<i>a</i> 0.0020	<i>b</i> 0.971	<i>c</i> 1.971	0.0039
0.1	0.16	0.0033			0.0065
		0.0050	0.956	1.956	0.0098
0.2	0.32	0.0067			0.0131
		0.0100	0.941	1.941	0.0194
0.3	0.48	0.0101			0.0196
0.4	0.64	0.0135			0.0262
0.5	0.80	0.0170			0.0327
		0.0200	0.922	1.922	0.0384
0.6	0.96	0.0205			0.0392
0.7	1.12	0.0240			0.0458
		0.0500	0.889	1.889	0.0915

^a The values in italics have been obtained from Noyes and Falk.

^b From Noyes and Falk.

^c This is the van't Hoff coefficient. It is obtained from the relation $i=1+(n-1) a$. For non-electrolytes its value is 1.

It was next necessary to calculate the volume-molecular concentrations (M) of potassium chloride that correspond to these values of iM . To do this an indirect method is required. If

the degree of dissociation of a salt is known for a given volume-molecular concentration, M , the particulate concentration, iM , may be calculated by means of the equation:

$$iM = 1 + (n-1) \alpha M.$$

In this equation n is the number of ions formed when a molecule of the salt is dissociated, and α (given just below) is the degree of ionization, or the fraction of the whole number of molecules that dissociates at a given concentration. For potassium chloride n has a value of 2, and the equation becomes:

$$iM = (1 + \alpha) M.$$

Values for the degree of ionization α of potassium chloride were obtained from Noyes and Falk's compilation,⁴³ based upon determinations of the conductance ratio. The volume-molecular concentrations (M) and the corresponding values of α are the italicized values given in the third and fourth columns, respectively. The corresponding values of iM for this salt, calculated by means of the last-mentioned formula, are the italicized values in the sixth column. Each of these italicized values in the sixth column represents the calculated osmotic concentration (iM), corresponding to a known volume-molecular concentration (M) of potassium chloride.

As has been explained, each of the values in roman type in the sixth column represents an osmotic concentration (iM) corresponding to an unknown volume-molecular concentration (M). These unknown values have been calculated by interpolation between the italicized values in the third column, assuming a linear relationship. The formula⁴⁴ used for this interpolation was the following:

$$M_0 = M_1 + [(iM)_0 - (iM)_1] \frac{M_2 - M_1}{(iM)_2 - (iM)_1}.$$

In this equation the two given values of M are M_1 and M_2 , the two given values of iM are $(iM)_1$ and $(iM)_2$, and the values to be interpolated are M_0 and $(iM)_0$, the value for $(iM)_0$ being derived from the formula:

$$(iM)_0 = \frac{\pi}{RT}$$

as described above.

⁴³ Noyes, A. A., and Falk, K. G., The properties of salt solutions in relation to the ionic theory. III. Electrical conductance, Journ. Am. Chem. Soc. 34 (1912) 474 and 475.

⁴⁴ See Ashton, C. H., Analytic Geometry. New York (1908) 35.

The interpolated values thus obtained for M_0 are inserted in roman type in the third column of the same table, and each of these is taken as the volume-molecular concentration of potassium chloride required to produce the corresponding partial osmotic pressure given in the second column. It will be seen that only these interpolated values were actually employed in making up the solutions. These are the values given in the second column of Table 2.

Similar calculations were made for each of the other three salts. The degrees of dissociation for calcium nitrate and magnesium sulphate were taken from Noyes and Falk, while those for monopotassium phosphate were obtained from Abbott and Bray.⁴⁵ The data used in making the calculations for these three salts will not be given here, but the final interpolated values are given in the last three columns of Table 2.

Many of the solutions used in this set were subjected to freezing-point determinations by the Beckmann method, in the same way that Shive⁴⁶ tested the total concentrations of Tottingham's and his own solutions. It was found that the lowering of the freezing point (Δ) for the solutions of this series varied from about 0.11° to 0.13° . Calculating the osmotic values corresponding to these limits, it appears that these values (for 25° C.) varied from about 1.50 to about 1.70 atmospheres.⁴⁷ The error in the osmotic value here introduced may be considered as negligible in this kind of work, for it will be recalled that those solutions were calculated to have an osmotic value of 1.60 atmospheres.

RESULTS OF SERIES I

Appearance of plants.—During the early part of the twenty-four-day period of series I most of the cultures were alike in appearance, although root development was noticeably retarded in some of the cultures as early as the time of the first renewal of solution. These injured cultures were the ones in solutions

⁴⁵ Abbott, G. A., and Bray, W. C., The ionization relations of ortho- and pyrophosphoric acids and their sodium salts, *Journ. Am. Chem. Soc.* 31 (1909) 729-763.

⁴⁶ Shive, J. W., The freezing points of Tottingham's nutrient solutions, *Plant World* 17 (1914) 345-353. Also, see Shive, J. W., *Am. Journ. Bot.* 2 (1915) 157-160.

⁴⁷ The following approximate formula was used for this calculation:

$$\pi_{25^\circ} = \frac{298}{273} 12.06 \Delta = 13.164 \Delta.$$

having high partial concentrations of magnesium sulphate, especially cultures T1R1C1 and T2R1C1. Growth, however, did not cease in these injured cultures, for the plants continued to enlarge slowly throughout the period. The solutions containing less magnesium sulphate produced much better growth and gave the most healthy appearing plants when the series was discontinued. During the latter part of the period these better cultures were seen to have much longer lateral roots and their tops were lighter green in color and noticeably larger than in the injured cultures.

Rather pronounced differences in the color of the plants in different cultures were apparent at the time of harvesting. The color ranged from a very deep shade of green to a light yellowish green. The plants in the cultures along the left-hand margins of triangle 1 and triangle 2 (fig. 1) were darkest green, while those along the right-hand margins of triangles 4, 5, and 6, and the culture of triangle 7 were the most chlorotic. In general, the depth of green decreased in passing from left to right in the triangles and in passing in the tetrahedron from triangle 1 to triangle 7. The largest tops were intermediate in color. Another morphological difference that appeared was a drying and bleaching of the tissue between the main veins, in some cultures resulting in longitudinal stripping of the leaves. This condition was limited to the cultures in solutions with low monopotassium phosphate content, especially rows 1, 2, and 3 of triangles 1 and 2.

A very similar symptom was observed by Tottingham in several of his four-salt solutions having an osmotic concentration of 8.15 atmospheres. This symptom was found in cultures having a high content of monopotassium phosphate, a maximum content of potassium nitrate, and approximately equal contents of calcium nitrate and magnesium sulphate. A thickening of the base of the stem with branching from the same region (perhaps equivalent to the "stooling" of wheat in the field) appeared in those cultures where root injury was most pronounced. Such branching of the wheat plant occurs normally in the field when the plants are considerably older than these plants were. It is suggested that those solutions which were unfavorable to root development also brought about symptoms of an earlier maturation of the plant.

The most pronounced morphological modification of the leaves appeared to be similar to that described by Tottingham as magnesium injury; this modification was also observed by Shive.

This form of leaf injury, which appeared in a few of the plants after about twelve days in the culture solutions and in more of them at the time of harvest, was characteristic of those cultures whose solutions had high ratios of magnesium sulphate to calcium nitrate. The two degrees of this injury, described by Shive as severe and as slight, were observed in this series and their distribution on the diagram is shown in fig. 2. In recording the occurrence of these two degrees of injury, when a spiral coiling was formed or the whole leaf was affected, the injury was considered severe; when no spiral was formed and not the whole leaf was affected, the injury was considered slight. In fig. 2 the cultures marked with crosses showed severe injury, and those marked with circles slight injury. The number of leaves injured, in the entire culture of six plants, is shown by the numeral placed near the point of the diagram.

Dry weights.—Since the roots and tops were weighed separately, two dry-weight data were obtained for each culture. The sum of these two weights, of course, gives the total dry weight of the plants in the cultures, but since this sum is generally controlled in its variation by the dry weight of tops, only the separate data for tops and for roots will be considered.

These data are presented in Table 4, in which the first column gives the culture number; the second, the data for tops; and the third, the data for roots. The dry weights are expressed as relative numbers, in terms of the value for the highest actual dry weight considered as 100. The actual dry weight for this culture is given in parentheses below the value 100. The actual dry weights may be obtained by means of this value.

High yields are indicated in the table by the letter H and low by the letter L. The method of defining high and low yields is as follows: The twenty-one cultures (one-fourth of the total number) giving highest yields are marked H, and the twenty-one giving lowest values are marked L. The remaining forty-two cultures (half of the total number) are considered as medium, excepting those which are numerically the same as the lowest of the "high" group which are marked H, and those which are the same as the highest of the "low" group which are marked L. The highest yield obtained in the series is indicated by gothic type, and the lowest by italics. The average relative yields obtained with Shive's and with Nottingham's best solutions, employed as controls in this series, are given at the bottom of the table, for comparison.

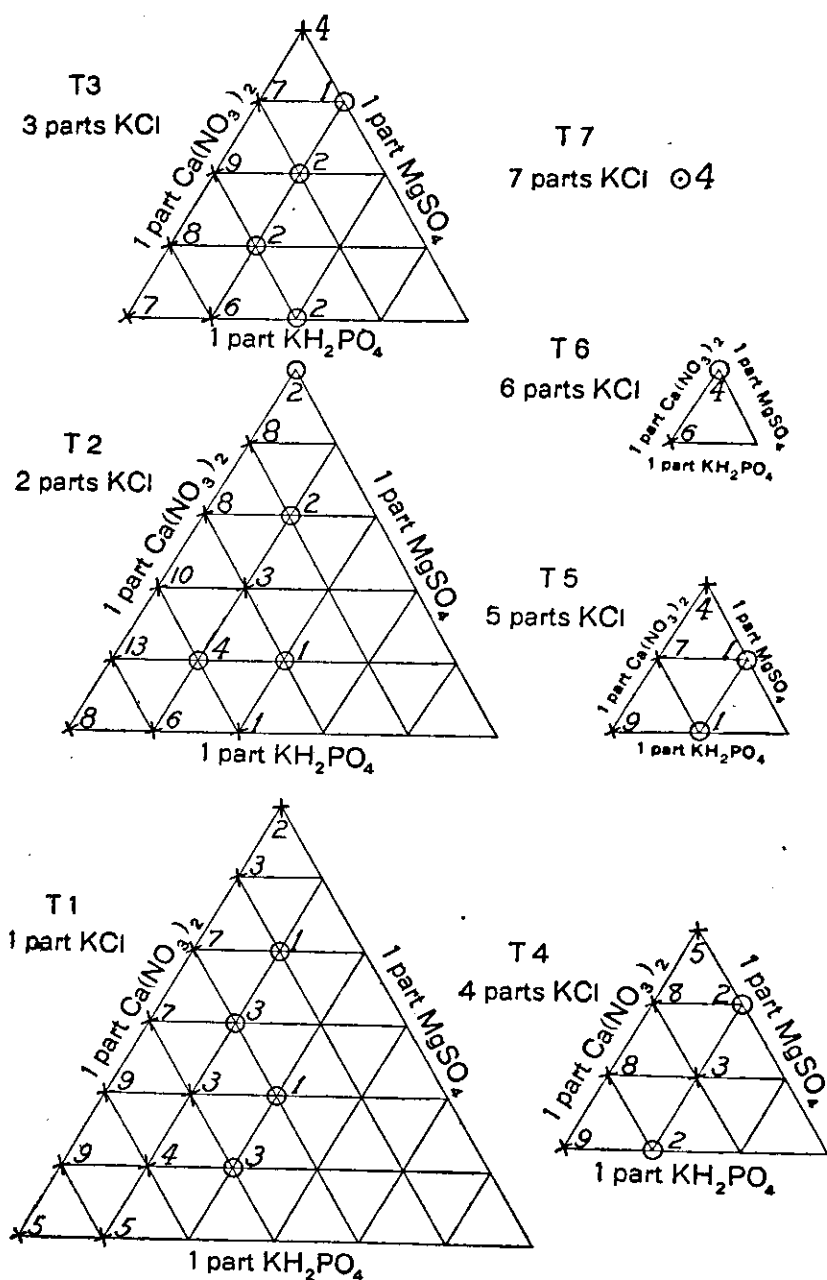


FIG. 2. Diagram for series I, showing leaf injury.

TABLE 4.—Relative dry weights of tops and roots of wheat; also, water-absorption data, and the amount of water absorbed for each gram of yield of tops and of roots (water requirement), relative to the highest as 100; for series I, conducted from January 11 to February 4, 1916.

Culture No.	Dry weight.		Water absorption.	Water requirement.	
	Tops (6 plants).	Roots (6 plants).		Tops.	Roots.
T1R1C1	60L	60L	53L	80L	66L
C2	71L	63L	82L	94H	88
C3	85	70	97H	94H	95H
C4	70L	58L	83	98H	98H
C5	80	54L	81L	81L	99H
C6	68L	55L	78L	93H	96H
C7	86	80H	87	84	74L
R2C1	74L	67	80L	89	82
C2	81	69	84	85	82
C3	82	60L	86	86	97H
C4	84	66	88	85	91H
C5	79	65L	82L	85	86
C6	83	80H	85	84	72L
R3C1	70L	63L	74L	87	80
C2	79	63L	80L	84	87
C3	85	63L	82L	79L	89H
C4	87H	62L	85	80L	93H
C5	81	77	80L	81L	71L
R4C1	77L	68	83	89	84
C2	89H	65L	88	81L	92H
C3	90H	69	89	82L	88
C4	79	67	80L	83	81
R5C1	77L	65L	83	89	87
C2	93H	66	89	78L	92H
C3	88H	76	90	83	81
R6C1	84	65L	85	82L	90H
C2	89H	66	89	82L	92H
R7C1	83	56L	80L	79L	98H
T2R1C1	71L	74	76L	88	71L
C2	72L	56L	74L	84	90H
C3	80	57L	83	85	100H (2058)
C4	78	67	93H	98H	95H
C5	86	74	94H	90	88
C6	81	69	83	85	83
R2C1	74L	66	80L	89	83
C2	85	61L	81L	78L	91H
C3	93H	75	97H	85	88
C4	88H	69	90	84	88
C5	85	78H	88	85	77L
R3C1	76L	65L	80L	87	84
C2	88H	65L	86	80L	90H
C3	87H	59L	83	79L	97H
C4	93H	85H	92H	82L	74L
R4C1	77L	62L	81L	87	89H
C2	100H	80H	100H	82L	85

TABLE 4.—Relative dry weights of tops and roots of wheat; also, water-absorption data, and the amount of water absorbed for each gram of yield of tops and of roots (water requirement), relative to the highest as 100; for series I, conducted from January 11 to February 4, 1916—Continued.

Culture No.	Dry weight.		Water absorption.	Water requirement.	
	Tops (6 plants).	Roots (6 plants).		Tops.	Roots.
	(.761)		344)		
T2R4C3	94H	85H	89	78L	72L
R5C1	82	70	87	87	85
C2	82	67	86	87	88
R6C1	94H	72	94H	82L	89H
T3R1C1	69L	72	80L	95H	75L
C2	75L	67	85	92H	86
C3	84	73	95H	93H	90H
C4	82	80H	96H	96H	82
C5	85	84H	95H	93H	77L
R2C1	77L	70	82L	88	80
C2	81	71	88	89	85
C3	86	67	89	85	90H
C4	80	79H	90	92H	77L
R3C1	83	81H	92H	91	78L
C2	90H	74	92H	85	85
C3	96H	100H	100H	86	68L
		(.245)	(344)		
R4C1	79	70	89	93H	87
C2	94H	85H	92H	81	74L
R5C1	82	70	86	87	84
T4R1C1	68L	68	80L	97H	80
C2	81	78H	92H	93H	81
C3	84	74	98H	96H	91H
C4	81	72	89	90	84
R2C1	80	80H	87	90	74L
C2	88H	70	88	82L	85
C3	87H	80H	98H	87	80
R3C1	89H	83H	94H	87	77L
C2	91H	78H	90	81L	78L
R4C1	91H	82H	98H	89	81
T5R1C1	78	82H	93H	99H	77L
C2	80	73	98H	95H	87
C3	82	84H	96H	96H	78L
R2C1	70L	69	79L	92H	79
C2	84	75	92H	90	83
R3C1	87H	85H	97H	82H	78L
T6R1C1	68L	73	82L	100H	77L
				(550)	
C2	82	80H	95H	95H	81
R2C1	74L	74	81L	90	75L
T7R1C1	71L	69L	82L	95H	82
Shive	90H	67L	90		
Tottingham	94H	89H	98H		

The yield data of Table 4 are presented graphically in fig. 1 (tops) and fig. 3 (roots). On these diagrams areas of high yields (H) are marked with small crosses, and those of low yields (L) are marked with small circles. The highest value in each case is shown by a large cross, and the lowest, by a large circle.

Water absorption.—The total amount of water absorbed by each culture was obtained by adding together the partial quantities recorded at the several changes of the solution. The sums thus obtained (relative to the greatest one) are shown in the fourth column of Table 4. Following the method employed for dry-weight data, the cultures giving high and low values are indicated by the letters H and L, respectively. The highest water-absorption value is indicated by gothic type and the lowest by italics.

Water requirement.—The amounts of water absorbed per unit of dry weight of tops and of roots were calculated for each culture. This ratio value is practically what has been termed the water requirement, and this term will be employed in this paper.⁴⁸ The last two columns of Table 4 present these data. The letters H and L are employed as heretofore, the highest value being again indicated by gothic type and the lowest by italics.

DISCUSSION OF SERIES I

Appearance of plants.—As has been mentioned, the plants appeared greener in color with solutions having higher partial concentrations of magnesium sulphate, which suggests a direct relation between the color and the amount of magnesium present in the cells. Furthermore, the color was more intense in the cultures having low partial concentrations of potassium chloride, or in those cultures in which the other three salts were present in relatively large amounts. The cultures with high partial concentrations of potassium chloride may be considered as those in which the plants were deprived in a large measure of the essential elements, excepting potassium.

Striping of the leaves occurred, as already described, with solutions having comparatively low potassium chloride values and very low monopotassium phosphate values.

⁴⁸ Briggs, L. J., and Shantz, H. L., The water-requirement of plants, II. A review of the literature, Bull. U. S. Dept. Agric., Bur. Pl. Ind. (1913) 285. Since practically all the water absorbed by such plants as those of the present experiments is given off by transpiration, the water-absorption data represent total transpiration.

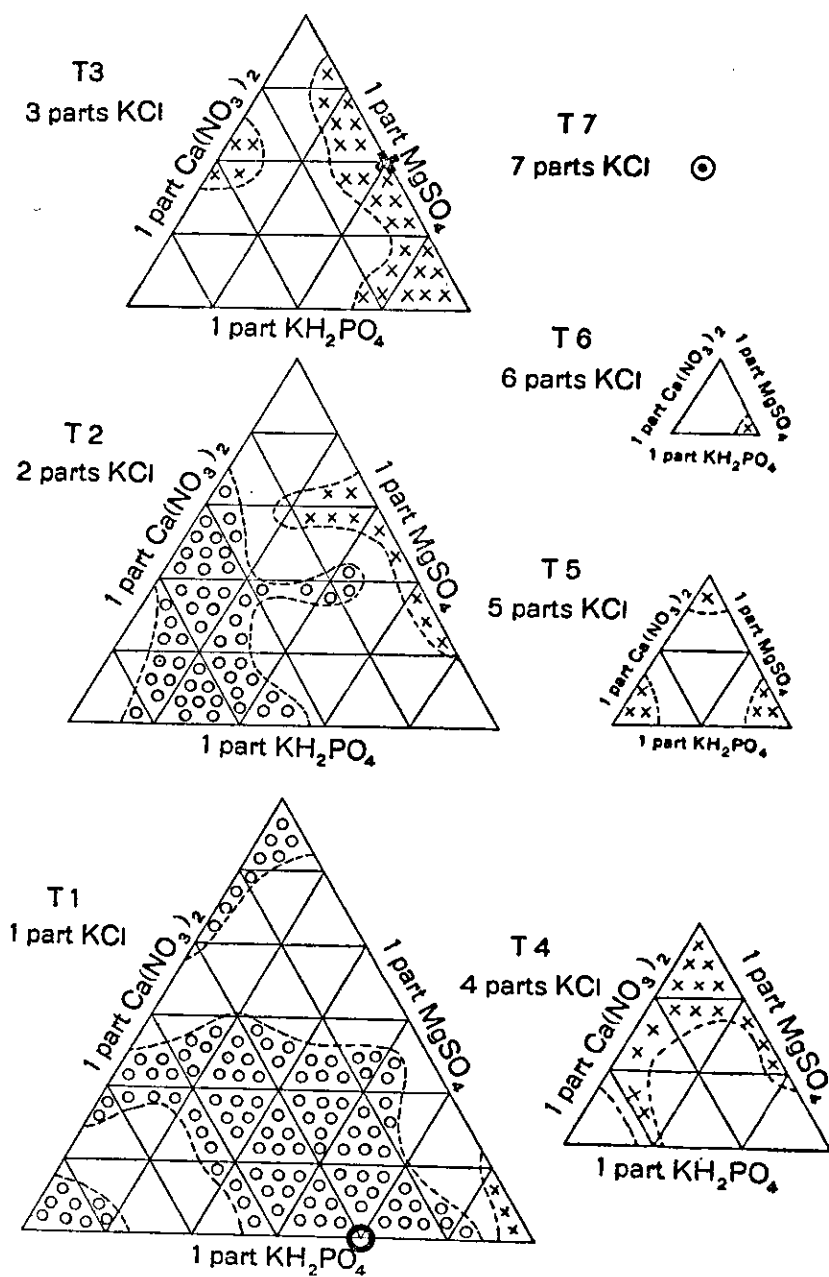


FIG. 8. Diagram for series I, showing relative dry weights of wheat roots.

Severe magnesium injury, pronounced root modifications, and the phenomenon resembling "stooling" were all clearly confined to solutions in which the ratio of magnesium to calcium lay between the limits 1.65 and 13.43; that is, in which the amount of magnesium sulphate was relatively high as compared with the amount of calcium nitrate. Of the remaining solutions, those in which the Mg/Ca-ratio value lay between the limits 0.81 and 3.64 showed slight magnesium injury. This form of injury in general was confined to the range of the ratio values from 0.81 to 13.43, and entire freedom from injury was shown in the cultures which had ratio values within the very narrow range from 0.21 to 0.81.

Shive found that when his three-salt solution had an osmotic value of 1.75 atmospheres the plants were free from magnesium injury with Mg/Ca-values of less than 1.5; and when the osmotic value was 4.00 atmospheres this limit occurred with the ratio value 2.2. From Tottingham's data it appears that no injury occurred with ratio values below 0.40, when the total osmotic value was 2.50 atmospheres; or below 0.28, when that value was approximately 8.00 atmospheres. This limiting value of the ratio Mg/Ca is thus seen to vary considerably according to the kinds of salts used, the salt proportions, and the total concentration of the solution. It may be added, however, that no case has been observed in the experimental studies here considered in which freedom from magnesium injury occurred with a ratio having a higher value than 2.90, except with solutions of very low total concentration where, Shive and Tottingham agree, none of this injury occurs at all with any value of this ratio.

Dry weights.—Inspection of the tetrahedral diagram of fig. 1 shows that the highest dry yield of tops was obtained in culture T2R4C2, having volume-molecular partial concentrations of the four salts as follows: 0.0067 M potassium chloride, 0.0138 M monopotassium phosphate, 0.0047 M calcium nitrate, and 0.0081 M magnesium sulphate. Lowest dry yield of tops (60 per cent of the highest) occurred in culture T1R1C1, having volume-molecular partial concentrations of the salts as follows: 0.0033 M potassium chloride; 0.0033 M monopotassium phosphate; 0.0023 M calcium nitrate; and 0.0309 M magnesium sulphate. The areas of low yields of tops occur in all triangles along the left-hand margins, corresponding to regions charac-

terized by low partial concentrations of calcium nitrate and high partial concentrations of magnesium sulphate.

The highest actual dry weights of tops obtained from these twenty-four-day cultures was 0.761 gram, and the lowest was 0.457 gram. The average dry yields of tops from three cultures each of Shive's and Tottingham's best solutions for wheat were 0.684 and 0.714 gram, respectively. It, therefore, appears that all three of these best solutions may be expected to give about the same yield of tops for wheat plants of this variety grown for twenty-four days under the general aërial conditions met with in the present series.

A few other points bearing on the top yields of this series will be mentioned in the discussion of series II.

With reference to root yields, the maximum dry weight was obtained in culture T3R3C3. In a general way, the areas of high and low root yields on the diagram (fig. 3) agree with the corresponding areas for top yields (fig. 1). The general truth of this statement is especially worthy of emphasis, because its opposite was true for the series of Shive and of Tottingham. It is possible that the addition of potassium chloride to the Shive three-salt solution resulted in altering in a fundamental way the relation between top yields and root yields.

Water absorption.—Greatest water absorption occurred with two cultures, T2R4C2, which also gave highest top yields, and culture T3R3C3, the latter culture having the following partial concentrations: 0.0101 M potassium chloride, 0.0103 M monopotassium phosphate, 0.0072 M calcium nitrate, and 0.0038 M magnesium sulphate. The lowest amount of water absorption occurred in culture T1R1C1, which also gave the lowest top yield and very low root yields. This very small water absorption appears undoubtedly related to the stunted tops and poor root development previously mentioned.

Triangular diagrams for water absorption (which is practically a measure of transpiration) have been omitted in the publication of this paper. But a comparison of such diagrams with those of figs. 1 and 3 (dry weights of tops and of roots, respectively) has shown that, in a very general way, the regions for high absorption correspond to those for high top and high root yields, all three occupying the areas of the triangles characterized by medium proportions of calcium and magnesium, and medium and low proportions of potassium chloride. This comparison has also shown that the areas of low water absorption generally correspond to areas of low top and root yields.

these low areas lying in the lower left-hand corners of the triangles, denoting solutions having high proportions of magnesium sulphate, and low proportions of calcium nitrate and monopotassium phosphate. The general proportionality between the transpiration and the dry yield reported by other workers was thus observed in these experiments. This relation is of course to be expected, since the ability of a particular set of plants to transpire depends principally upon the leaf surface of the plants; this is measured approximately by their dry weight, and the amount of water absorbed is a measure of their transpiration.⁴⁹

Water requirement.—The highest water requirement for tops (Table 4) was found to be that for culture T6R1C1, having 0.6 of its total osmotic concentration due to potassium chloride. Three quite different cultures showed the lowest water requirement for tops. These were cultures T1R5C2, T2R2C2, and T2R4C3. There is very little in common between these cultures, as regards the proportions of the salts. Triangular diagrams, omitted in this publication, have shown that areas of high water requirements for tops occur in all of the triangles; that is, with all proportions of potassium chloride tested. These areas lie in almost all cases along the lower margins of the triangles, and are thus restricted to cultures having very low partial concentrations of monopotassium phosphate. On the other hand, low water requirements are in general associated with high relative proportions of monopotassium phosphate. In a very general way, solutions which gave high water requirements of tops also gave high top yields and, conversely, those which gave low water requirements gave low top yields. No relation is apparent between high water requirement of tops and either water absorption or root yields.

Turning now to water requirement of roots, it is seen that culture T2R1C3 showed the highest value, while culture T1R1C1 showed the lowest value. High values were not found in this series for solutions having more than 0.4 of their total concentration due to potassium chloride. There is no evident general correlation between either high or low values and the proportions of the various nutrient salts. A comparison of the triangular diagrams, representing water requirement of roots, with fig. 3 has shown that there is a suggestion of an inverse relationship

⁴⁹ Livingston, B. E., Relation of transpiration to growth in wheat, *Bot. Gaz.* 40 (1905) 178-195.

between the water requirement of roots and the dry weight of roots. Likewise, there is, in the present results, a tendency for the water requirement of roots to be inversely related to water absorption. There appears to be little or no relationship between the water requirement of roots and either the dry weight or the water requirement of tops.

SERIES II

METHODS OF SERIES II

This series was conducted for twenty-four days, from February 12 to March 7, 1916. The highest temperature recorded during this period was 28° C. (February 14, 22, 28) and the lowest was 10° C. (February 13). The average daily maximum temperature for the period was 25°, and the average daily minimum was 16° C. The corrected water loss from the spherical porous-cup atmometer showed a daily mean of 17.5 cubic centimeters and a total loss of 241 cubic centimeters for the entire period. This series was carried out in duplicate, so that there were two simultaneous cultures of six plants each for each of the sets of salt proportions tested.

The plan of this series was similar to that followed for series I. The same four salts were employed and the solutions also had the same total osmotic concentration (1.60 atmospheres) as before. In series II it was planned to cover the range of salt proportions used in series I without repeating all of the cultures. Forty selected solutions were used. Their composition may be represented by the same kind of diagrams as were used for series I. The numbers and positions upon the diagram of these selected solutions are shown in fig. 4, the culture solutions here used being represented by dots. It will be seen that solutions from all of the triangles are included. The method of designation is the same as in series I, but fractional numbers must be used to designate solutions which do not fall upon the points of intersection of the lines. In solution T2R4 $\frac{3}{4}$ C1 $\frac{3}{4}$, for example, the four salts contribute the following portions of the total osmotic concentration: Potassium chloride, 0.2; monopotassium phosphate, 0.4 $\frac{3}{4}$; calcium nitrate, 0.1 $\frac{3}{4}$; and magnesium sulphate, 0.1 $\frac{3}{4}$. For comparison, Shive's best three-salt solution for wheat and Tottingham's best four-salt solution were again used.

TABLE 5.—Partial concentrations of potassium chloride, monopotassium phosphate, calcium nitrate, and magnesium sulphate in each of the solutions employed in series II; also, the values of the three cation ratios; total osmotic value of each solution, 1.60 atmospheres.

Culture No.	Volume-molecular concentration.				Cation-ratio value.		
	KCl.	KH ₂ PO ₄ .	Ca(NO ₃) ₂ .	MgSO ₄ .	Mg/Ca.	Mg/K.	Ca/K.
	M.	M.	M.	M.			
T1R1C1	0.0033	0.0033	0.0023	0.0309	13.43	4.68	0.35
T1R1C4	0.0033	0.0033	0.0098	0.0171	1.75	2.59	1.48
T1R1C7	0.0033	0.0033	0.0117	0.0038	0.21	0.58	2.68
T1R2C2	0.0033	0.0068	0.0047	0.0216	4.60	2.14	0.47
T1R2C5	0.0033	0.0068	0.0124	0.0081	0.65	0.80	1.22
T1R3C3	0.0033	0.0103	0.0072	0.0126	1.75	0.93	0.53
T1R4C1	0.0033	0.0138	0.0023	0.0171	7.44	1.00	0.13
T1R4C4	0.0033	0.0138	0.0098	0.0038	0.39	0.22	0.57
T1R5C2	0.0033	0.0172	0.0047	0.0081	1.72	0.39	0.23
T1R7C1	0.0033	0.0243	0.0023	0.0038	1.65	0.14	0.08
T2R1C1	0.0067	0.0033	0.0023	0.0261	11.35	2.61	0.23
T2R1C3	0.0067	0.0033	0.0085	0.0149	1.75	1.49	0.85
T2R1C6	0.0067	0.0033	0.0150	0.0038	0.25	0.38	1.50
T2R1C1	0.0067	0.0056	0.0039	0.0201	5.15	1.63	0.32
T2R1C4	0.0067	0.0056	0.0115	0.0067	0.58	0.54	0.93
T2R2C2	0.0067	0.0091	0.0064	0.0111	1.73	0.70	0.41
T2R3C1	0.0067	0.0121	0.0023	0.0149	6.48	0.79	0.12
T2R3C3	0.0067	0.0121	0.0085	0.0038	0.45	0.20	0.46
T2R4C1	0.0067	0.0161	0.0039	0.0067	1.72	0.29	0.17
T2R6C1	0.0067	0.0208	0.0023	0.0038	1.65	0.14	0.08
T3R1C1	0.0101	0.0033	0.0023	0.0216	9.39	1.61	0.17
T3R1C3	0.0101	0.0033	0.0072	0.0126	1.75	0.94	0.54
T3R1C5	0.0101	0.0033	0.0124	0.0038	0.31	0.28	0.93
T3R1C1	0.0101	0.0056	0.0039	0.0156	4.00	0.99	0.25
T3R1C3	0.0101	0.0056	0.0089	0.0067	0.75	0.43	0.57
T3R2C2	0.0101	0.0080	0.0055	0.0096	1.75	0.53	0.80
T3R3C1	0.0101	0.0103	0.0023	0.0126	5.48	0.62	0.11
T3R3C3	0.0101	0.0103	0.0072	0.0038	0.53	0.19	0.35
T3R3C1	0.0101	0.0126	0.0039	0.0067	1.72	0.30	0.17
T3R5C1	0.0101	0.0173	0.0023	0.0038	1.65	0.14	0.08
T4R1C1	0.0135	0.0033	0.0023	0.0171	7.44	1.02	0.14
T4R1C4	0.0135	0.0033	0.0098	0.0038	0.39	0.23	0.58
T4R2C2	0.0135	0.0068	0.0047	0.0081	1.72	0.40	0.23
T4R4C1	0.0135	0.0138	0.0023	0.0038	1.65	0.14	0.08
T5R1C1	0.0170	0.0033	0.0023	0.0126	5.48	0.62	0.11
T5R1C3	0.0170	0.0033	0.0072	0.0038	0.53	0.19	0.35
T5R1C1	0.0170	0.0056	0.0039	0.0067	1.72	0.30	0.17
T5R3C1	0.0170	0.0103	0.0023	0.0038	1.65	0.14	0.08
T6R1C1	0.0205	0.0045	0.0031	0.0052	1.68	0.21	0.12
T7R1C1	0.0240	0.0033	0.0023	0.0038	1.65	0.14	0.08

The chemical composition of each of the forty solutions in series II is shown in Table 5, which corresponds in arrangement to Table 1. The calculation for this series followed the general method employed in series I and resulted in the partial molecular concentrations given in Table 6, which were used directly in the preparation of Table 5.

TABLE 6.—Partial concentration of each of the four salts required to produce from 0.1 to 0.7 of the total osmotic concentration of 1.60 atmospheres; for series II.

Fractional parts of 1.60 atmospheres.	Salt.			
	KCl.	KH ₂ PO ₄ .	Ca(NO ₃) ₂ .	MgSO ₄ .
	<i>M.</i>	<i>M.</i>	<i>M.</i>	<i>M.</i>
0.1	0.0033	0.0033	0.0023	0.0038
0.1½	-----	0.0045	0.0031	0.0052
0.1¾	-----	0.0056	0.0039	0.0067
0.2	0.0067	0.0068	0.0047	0.0081
0.2½	-----	0.0080	0.0055	0.0096
0.2¾	-----	0.0091	0.0064	0.0111
0.3	0.0101	0.0103	0.0072	0.0126
0.3½	-----	0.0121	0.0085	0.0149
0.3¾	-----	0.0126	0.0089	0.0156
0.4	0.0135	0.0138	0.0098	0.0171
0.4½	-----	0.0161	0.0115	0.0201
0.5	0.0170	0.0173	0.0124	0.0216
0.6	0.0205	0.0208	0.0150	0.0261
0.7	0.0240	0.0243	0.0177	0.0309

RESULTS OF SERIES II

Appearance of plants.—Root and top development took place in a way very similar to that described for the preceding series. The various differences in the appearance of the plants described as occurring in series I were observed in the present series to about the same degree with reference to the range of salt proportions. The distribution of the two forms of magnesium injury in this series is shown by the diagrams of fig. 5, which is to be interpreted like fig. 2.

Dry weights.—The dry weight data for this series are shown in Table 7, in which the various items are arranged as in Table 4, excepting that in the present case the actual values corresponding to the two duplicate cultures are given, followed by the relative average. Thus these relative average weights correspond to the relative weights given in Table 4. The letters H and L are used in the same way as in the preceding series, but it will of course be noted that the "high" and the "low"

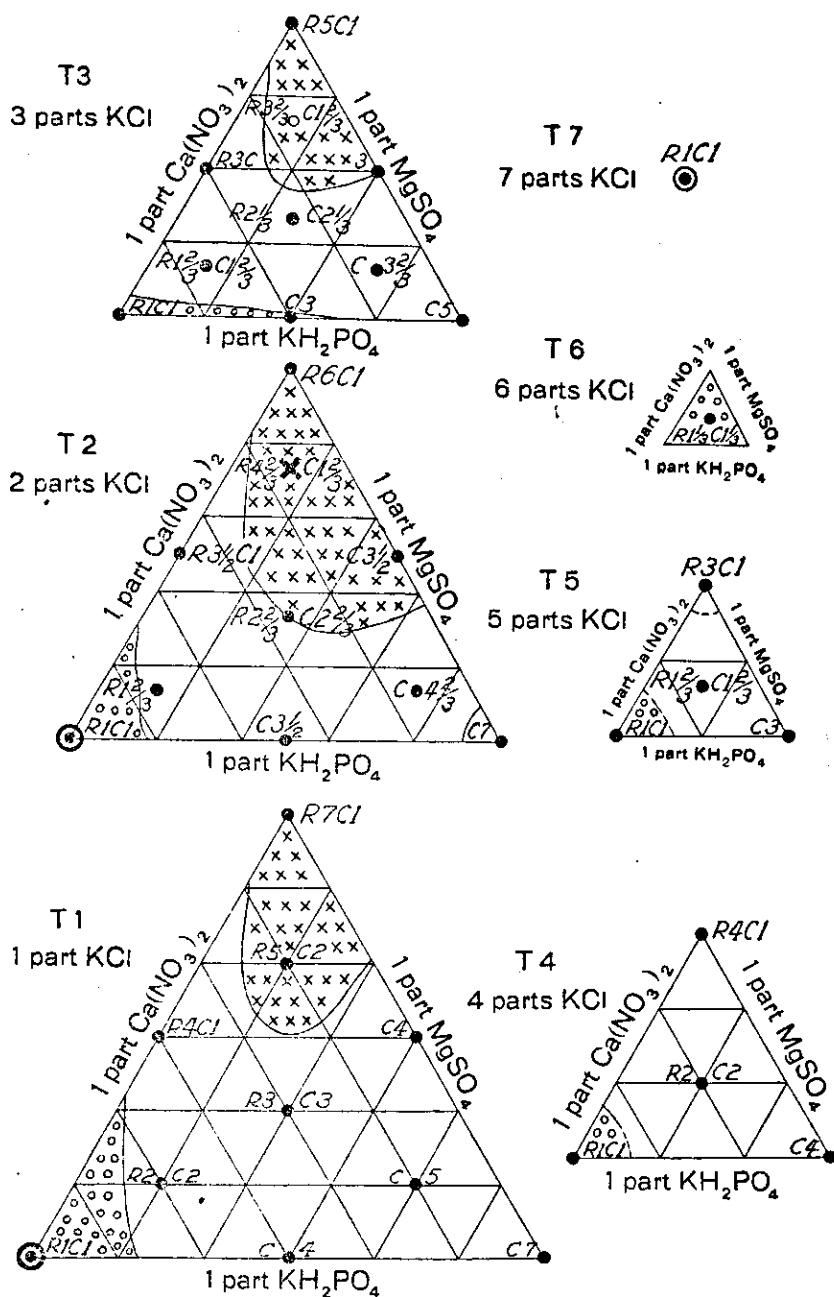


FIG. 4. Diagram for series II, showing culture numbers and osmotic proportions of the four salts.

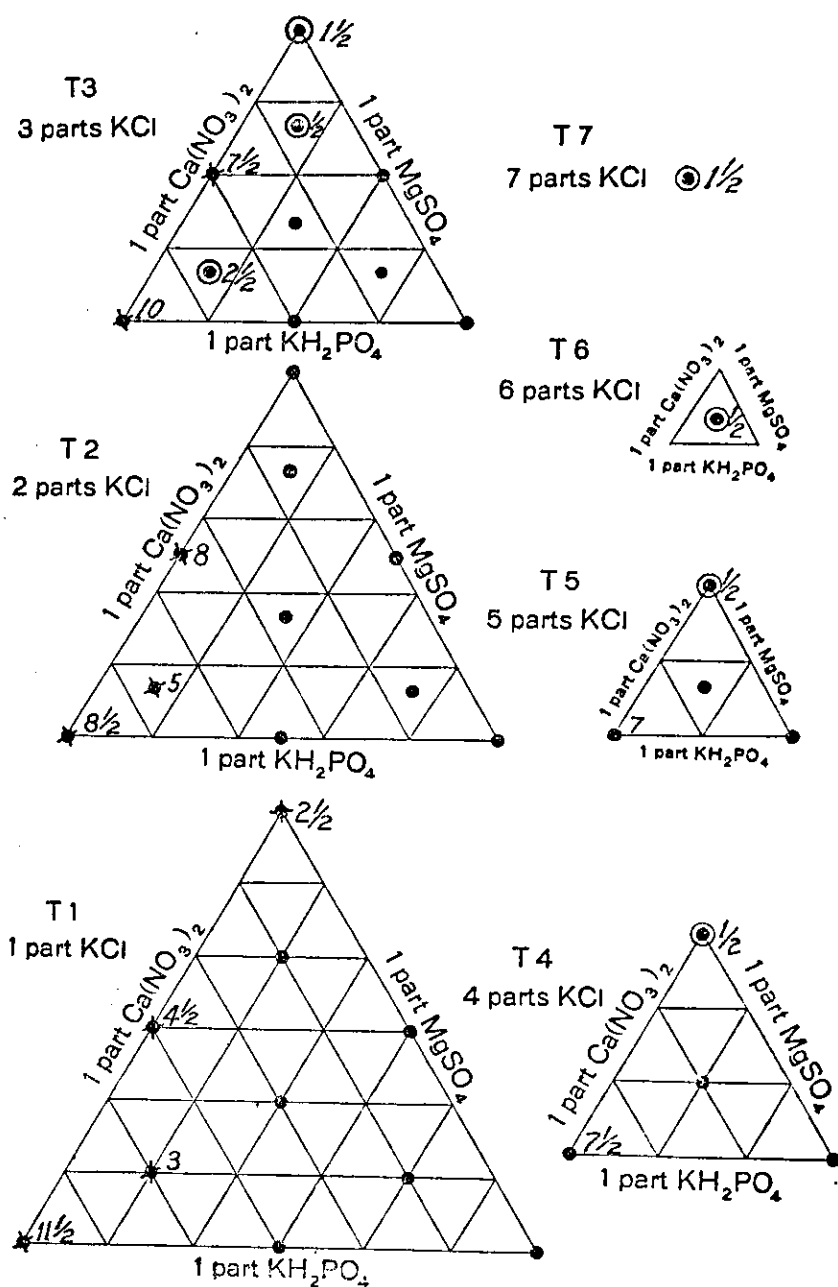


FIG. 5. Diagram for series II, showing leaf injury.

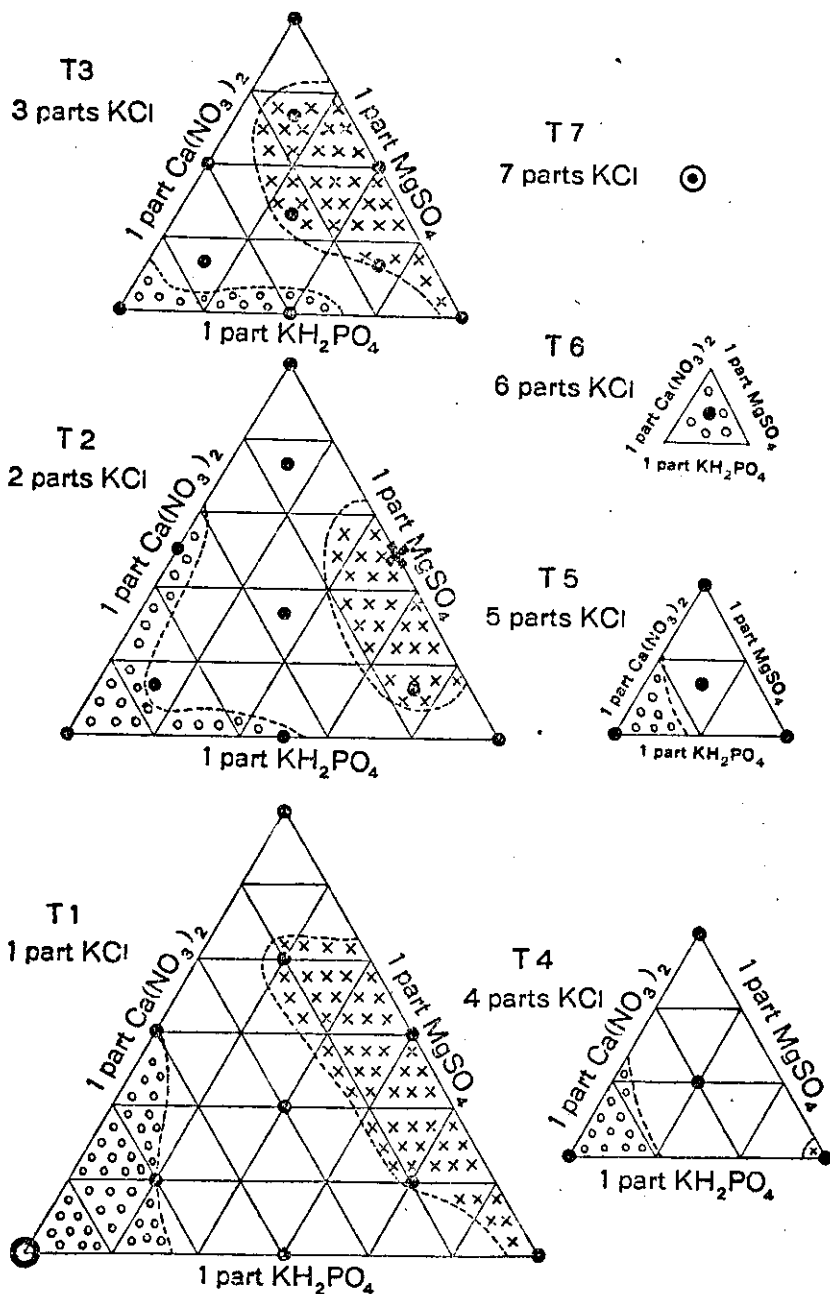


FIG. 6. Diagram for series II, showing relative dry weights of wheat roots.

groups here primarily include ten cultures each, instead of twenty-one as in the other case. The relative average yields simultaneously obtained with Shive's and with Tottingham's best solutions are again given at the bottom of the table. The data of Table 7 are shown diagrammatically in fig. 4 (tops) and fig. 6 (roots), in which the method of plotting is the same as that for series I (figs. 1 and 3.)

Water absorption.—The data of the total water absorption for each of the cultures in this series are shown in Table 8, where arrangement and notation are the same as heretofore followed.

Water requirement.—The relative average values for the amounts of water absorbed per unit of dry weight of tops and of roots are also presented in Table 8.

DISCUSSION OF SERIES II

Appearance of plants.—The appearance of the plants and the occurrence of magnesium injury were practically the same as in series I, and these features need not be discussed in detail.

Dry weights.—The distribution of the high and low values of top yields on the diagram for this series (fig. 4) agrees in general with the distribution of these values for series I (fig. 1). The highest yields of tops for series II was 0.804 gram for culture T2R4 $\frac{2}{3}$ C1 $\frac{1}{3}$, which had virtually the same salt proportions as the one giving the highest yield in series I (T2R4C2). Culture T1R1C1 gave the lowest top yield in series I and in both the duplicates of series II. The lowest yields for the two duplicates of series II were 0.573 and 0.529 gram (an average of 69 per cent of the highest), while the corresponding lowest yield for series I (carried out earlier in the winter) was 0.457 gram. In a similar way, the two duplicates giving the highest yield in series II (culture T2R4 $\frac{2}{3}$ C1 $\frac{1}{3}$) were 0.804 and 0.803 gram, while the highest yield from series I (culture T2R4C2) was 0.761 gram. This suggests that the aërial conditions for the two series were such as to give a somewhat higher yield of tops in the second series. The average top yield for four parallel cultures of Shive's best solution was 0.801 gram, practically the same as the best yield from the series with chloride. This value was also markedly higher than the corresponding value (0.684 gram) for the Shive solution in series I. A similar, though less pronounced, difference between the average top yields for Tottingham's solution in series I (0.714 gram) and in series II (0.751 gram) may be noticed. As far as these

data go, it appears that Tottingham's best solution gave a somewhat higher top yield than did Shive's in series I, while this relation was reversed in series II. On the whole, however, the best three salt proportions seem to be about the same in their ability to produce dry top yields under the aerial conditions of both these series.

As has been said, the salts used in the present study are the same as those of the solution that has come to be known as Detmer's solution.⁵⁰ This contains the four salts in the following proportions: 0.0130 M calcium nitrate, 0.0039 M monopotassium phosphate, 0.0044 M magnesium sulphate, and 0.0072 M potassium chloride. These exact proportions were not tested in the present work, but there were two solutions, in both series I and series II, the proportions of which closely resembled those used by Detmer. These were T2R1C6 and T3R1C5. These two solutions resembling Detmer's gave only 81 and 85 per cent of the top yield obtained with the best proportions in series I (solution T2R4C2); and these same solutions gave only 77 and 81 per cent of the top yields obtained with the best proportions in series II (solution T2R4 $\frac{2}{3}$ C1 $\frac{2}{3}$). In series I, at least thirty of the eighty-four solutions tested gave higher yields of tops than were obtained with the solutions closely resembling Detmer's in salt proportions. An even more marked improvement over the growth obtained with Detmer's exact proportions is reported by Shive for his best three-salt solution which, as has been mentioned, gave practically the same yield as did the best four-salt solution used in this study.

Regarding the production of root yields, the same generalizations appear to hold for series II as were stated for series I; and the general correspondence between high and low root areas, on the one hand, and between high and low top areas, on the other hand, seems to be more definite in the latter series. The salt proportions giving the lowest root yields were the same in both series (T1R1C1), and these same proportions also gave lowest top yields in both. In series II the highest root yield occurred in culture T2R3 $\frac{1}{2}$ C3 $\frac{1}{2}$, which had nearly the same salt proportions as the culture giving highest root yields in series I (T3R3C3).

⁵⁰ Detmer, W., *Practical Plant Physiology*. Translated by S. A. Moor. London (1898) 2.

TABLE 7.—Actual and relative average dry weights of tops and roots of wheat; for series II, conducted from February 12 to March 7, 1916.

Culture No.	Tops (6 plants).			Roots (6 plants).		
	A. actual.	B. actual.	Average, relative.	A. actual.	B. actual.	Average, relative.
T1R1C1	0.573	0.529	69 L	0.175	0.176	56 L
T1R1C4	0.699	0.658	84	0.244	0.218	74
T1R1C7	0.586	0.621	75 L	0.264	0.307	91 H
T1R2C2	0.728	0.685	88	0.223	0.212	69 L
T1R2C3	0.690	0.644	83	0.283	0.217	80 H
T1R3C3	0.732	0.733	91	0.224	0.231	73
T1R4C1	0.710	0.673	86	0.221	0.213	69 L
T1R4C4	0.667	0.748	88	0.256	0.305	89 H
T1R5C2	0.783	0.735	94 H	0.269	0.238	81 H
T1R7C1	0.780	0.772	97 H	0.256	0.225	77
T2R1C1	0.522	0.582	69 L	0.187	0.180	59 L
T2R1C3	0.628	0.663	80	0.203	0.210	66 L
T2R1C6	0.631	0.608	77 L	0.237	0.244	77
T2R1C1	0.689	0.670	85	0.212	0.237	72
T2R1C4	0.682	0.699	86	0.248	0.275	83 H
T2R2C2	0.744	0.738	92 H	0.231	0.242	76
T2R3C1	0.655	0.683	83	0.203	0.224	68 L
T2R3C3	0.741	0.782	95 H	0.305	0.323	100 H (.314)
T2R4C1	0.804	0.803	100 H (.804)	0.230	0.234	74
T2R6C1	0.756	0.803	97 H	0.222	0.243	74
T3R1C1	0.601	0.632	77 L	0.209	0.221	68 L
T3R1C3	0.615	0.605	76 L	0.212	0.209	67 L
T3R1C5	0.635	0.661	81	0.287	0.285	91 H
T3R1C1	0.735	0.709	90	0.244	0.240	77
T3R1C3	0.720	0.628	84	0.257	0.245	80 H
T3R2C2	0.739	0.720	91	0.264	0.244	81 H
T3R3C1	0.651	0.749	87	0.237	0.257	79
T3R3C3	0.762	0.719	92 H	0.327	0.284	97 H
T3R3C1	0.755	0.778	95 H	0.273	0.247	83 H
T3R5C1	0.775	0.727	93 H	0.220	0.232	72
T4R1C1	0.589	0.582	73 L	0.213	0.189	64 L
T4R1C4	0.632	0.615	78	0.248	0.256	80 H
T4R2C2	0.655	0.699	84	0.227	0.242	76
T4R4C1	0.744	0.677	88	0.251	0.221	75
T5R1C1	0.543	0.614	72 L	0.194	0.204	63 L
T5R1C3	0.608	0.658	79	0.223	0.230	72
T5R1C1	0.665	0.678	84	0.256	0.222	76
T5R3C1	0.736	0.736	92 H	0.239	0.241	76
T6R1C1	0.622	0.609	77 L	0.211	0.213	68 L
T7R1C1	0.623	0.537	72 L	0.227	0.208	69 L
Shive			100 H			70
Tottingham			93 H			93 H

TABLE 8.—Water-absorption data for wheat; also, amount of water absorbed for each gram of yield of tops and of roots (water requirement), relative to the highest average as 100; for series II, conducted from February 12 to March 7, 1916.

Culture No.	Water absorption.			Water require- ment.	
	A. actual.	B. actual.	Average, relative.	Tops, average, relative.	Roots, average, relative.
	cc.	cc.			
T1R1C1	304	283	73L	81	94H
T1R1C4	408	382	98H	81	97H
T1R1C7	417	375	99H	100H (656)	78L
T1R2C2	378	350	91L	79L	94H
T1R2C5	391	339	91L	83	88L
T1R3C3	386	372	94	79L	94H
T1R4C1	355	351	88L	78L	92
T1R4C4	380	357	92	79L	74L
T1R5C2	406	384	98H	79L	88
T1R7C1	394	374	96	75L	90
T2R1C1	304	304	76L	84	93
T2R1C3	380	352	91L	86	100H (1768)
T2R1					
T2R1C6	369	364	91L	90H	86L
T2R1½C1½	382	372	94	84	95H
T2R1½C4½	400	373	96	85	84L
T2R2½C2½	398	363	95	78L	91
T2R3½C1	363	326	86L	79L	91
T2R3½C3½	399	388	98H	79L	71L
T2R4½C1½	380	374	94	72L	92
T2R6C1	390	362	94	74L	91
T3R1C1	363	342	88L	87H	93
T3R1C3	369	363	91L	91H	98H
T3R1C5	414	389	100H (402)	95H	79L
T3R1½C1½	399	385	98H	83	92
T3R1½C3½	388	382	96	87H	87L
T3R2½C2½	403	393	99H	83	89
T3R3C1	410	368	97H	85	89
T3R3C3	417	386	100H	83	74L
T3R3½C1½	402	374	97H	77L	84L
T3R5C1	373	363	92	75L	92
T4R1C1	341	337	84L	88H	95H
T4R1C4	400	394	99H	97H	89
T4R2C2	388	367	94	85	91
T4R4C1	383	356	92	79L	89
T5R1C1	354	333	86L	91H	92H
T5R1C3	382	371	94	91H	94H
T5R1½C1½	397	359	94	86	90
T5R3C1	383	382	95	79L	90
T6R1½C1½	360	343	88L	87H	94H
T7R1C1	366	335	87L	92H	91
Shive			95	72L	90
Tottingham			98H	80	77L

From the dry-weight data of both series I and series II it appears that for a given total concentration these plants were not very sensitive to small differences in the salt proportions. A relatively large number of salt combinations in both series I and series II gave approximately equal growth, with apparently identical conditions other than those in the nutrient solution. Thus in series I eleven other solutions gave at least nine-tenths as high dry yields of tops as did the best solution; and in series II twelve other solutions gave at least nine-tenths of the yield of tops obtained in the best solution. The individual differences between the different plants in a culture is probably the greatest factor in determining just which set of a number of very favorable sets of salt proportions will give the very highest yield.

The relation between the cation-ratio values and the yields of wheat tops for series I and II are shown in Table 9. It will be seen that for low yields of tops the Mg/Ca-ratio values cover practically the whole range of these values for the entire series. There is thus no relation between the value of the Mg/Ca-ratio and the low yield of tops. The same thing is also true of the values of the Mg/K- and Ca/K-ratios, since all tested values of these ratios give low yields in some cultures.

TABLE 9.—Cation-ratio values for solutions of series I and II; for the entire series, and for solutions giving high and low and highest and lowest top yields.

	Mg/Ca.		Mg/K.		Ca/K.	
	Series I.	Series II.	Series I.	Series II.	Series I.	Series II.
Entire series:						
Minima	0.21	0.21	0.14	0.14	0.08	0.08
Maxima	13.43	13.43	4.68	4.68	2.68	2.68
Range	13.22	13.22	4.54	4.54	2.60	2.60
Low yields:						
Minima	0.54	0.21	0.14	0.14	0.08	0.08
Maxima	13.43	13.43	4.68	4.68	2.27	2.68
Range	12.89	13.22	4.54	4.54	2.19	2.60
High yields:						
Minima	0.53	0.53	0.14	0.14	0.08	0.08
Maxima	3.52	1.73	0.93	0.70	0.73	0.45
Range	2.99	1.20	0.79	0.66	0.65	0.37
Highest yields	1.72	1.72	0.40	0.29	0.23	0.17
Lowest yields	13.43	13.43	4.68	4.68	0.35	0.35
Do		11.35		2.61		0.23

For high yields of tops, however, there does appear to be a certain relation between cation-ratio values and yield. High

yields of tops were restricted to cultures having values of the Mg/Ca-ratio ranging from 0.53 to 3.52 for series I, and from 0.53 to 1.73 for series II, while the total range for each of these entire series was from 0.21 to 13.43. Thus high yields of tops were never obtained when the Mg/Ca-ratio value was above 3.52, no matter what the proportions of the other ions. High yields of tops were obtained when the Mg/K-ratio had the lowest value tested (0.14), and were restricted to relatively low values of this ratio. The highest value of the Mg/K-ratio that gave high yields was 0.93, while the highest value tested was 4.64. High yields of tops were also restricted to low values of the Ca/K-ratio, never being obtained when this was higher than 0.73, while the highest value for the entire series was 2.68. The very lowest value (0.08) of the Ca/K-ratio also produced high yields of tops. The data presented in this table may be summarized by stating that low yields were obtained with practically all ratio values tested; but that high yields were never obtained when the Mg/Ca-ratio was higher than 3.52, nor when the Mg/K-value was above 0.93, nor when the Ca/K-value was above 0.73.

Culture T1R1C1, which gave the lowest yields of tops in series I and II, had the following ratio values: Mg/Ca, 13.43; Mg/K, 4.68; Ca/K, 0.35. The other culture in series II giving a yield as low as T1R1C1 (namely culture T2R1C1) had the following values: Mg/Ca, 11.35; Mg/K, 2.61; and Ca/K, 0.23. The highest yields of tops were obtained, in series I, with culture T2R4C2 having the following ratio values: Mg/Ca, 1.72; Mg/K, 0.40; Ca/K, 0.23; and in series II, with culture T2R4½C1½ having the ratio values: Mg/Ca, 1.72; Mg/K, 0.29; Ca/K, 0.17. These two solutions are characterized by equal Mg/Ca-ratios; but the other two ratios are different for the two solutions.

The relations between cation-ratio values and root yields for series I and II are shown in Table 10. Considering the results of the two series together, it is apparent that there is little or no relation between low root yield and the value of any one of the three cation ratios. This agrees with what was found for top yields. However, as in the case of top yields, there was an apparent relation between high yields and cation-ratio values. Thus, high root yields were obtained only when the Mg/Ca-ratio had values from 0.21 to 5.48, while the total range for the series was from 0.21 to 13.43. In a similar way high root yields were restricted to low values of the Mg/K-ratio, from 0.14 to 0.80, and never occurred with ratio values between 0.80 and 4.68. On the other hand, there was no relation between high

root yields and the Ca/K-ratio values, high yields being obtained with the whole range of these values tested.

The general conclusion which must be reached from these experiments is similar to that already stated by Gile,⁵¹ by Tottingham, and by Shive. The effect of a certain ratio between any two ions in a certain total concentration appears to depend upon the relation of these ions to all the other ions in the nutrient solution; that is, upon the complex balance of ions in the nutrient solution. A certain optimum ratio may be found between two ions, as calcium and magnesium, for example, when a certain balance exists between all the other ions present. But if this balance is altered, the optimum ratio between calcium and magnesium, for example, would be altered.

TABLE 10.—*Cation-ratio values for solutions of series I and II; for the entire series, and for solutions giving high and low and highest and lowest root yields.*

	Mg/Ca.		Mg/K.		Ca/K.	
	Series I.	Series II.	Series I.	Series II.	Series I.	Series II.
Entire series:						
Minima	0.21	0.21	0.14	0.14	0.08	0.08
Maxima	13.43	13.43	4.68	4.68	2.68	2.68
Range	13.22	13.22	4.54	4.54	2.60	2.60
Low yields:						
Minima	0.54	1.65	0.14	0.14	0.08	0.08
Maxima	13.43	13.43	4.68	4.68	2.27	0.85
Range	12.89	12.78	4.54	4.54	2.19	0.77
High yields:						
Minima	0.81	0.21	0.14	0.19	0.08	0.17
Maxima	5.48	1.75	0.75	0.80	2.68	2.68
Range	5.17	1.54	0.61	0.61	2.60	2.51
Highest yields	0.53	0.45	0.19	0.20	0.35	0.45
Lowest yields	1.02	13.43	1.91	4.68	1.88	0.85

Water absorption.—Cultures T3R1C5 and T3R3C3 absorbed the greatest quantities of water in this series; the latter culture also absorbed the most in series I. This series agrees with series I in the culture showing lowest water absorption (T1R1C1). In a general way, also, there is an agreement between the two series in the direct relationship shown between dry yields of tops and roots, on the one hand, and water absorption on the other.

Water requirement.—The results of this series disagreed with those of the preceding one in the exact proportions giving high-

⁵¹ Gile, P. L., Lime-magnesia ratio as influenced by concentration, Bull. Porto Rico Agric. Exp. Sta. 12 (1912).

est and lowest top and highest and lowest root water requirements, though there was general agreement between the high and low and medium areas for the two series. The general features are the same as those for the preceding series and will not be discussed in detail here.

SERIES III

METHODS OF SERIES III

Series III extended over thirty-two days, from December 4, 1916, to January 5, 1917. The maximum temperature for this period was 28° C. (December 8, 13, 14, 21), and the minimum was 12° C. (December 15, 17, 30). The average daily maximum for the period was 25° C., and the average daily minimum was 16° C. The mean daily water loss from the atomometer was 15.7 cubic centimeters, and the total loss for the period was 501 cubic centimeters.

All of the culture solutions employed in this series had the same total concentration (1.60 atmospheres) as was used in series I and II. But much higher partial concentrations of potassium chloride were included in this series, since the results obtained from the preceding series showed no very pronounced effects that might be attributed to potassium chloride. Four sets of culture solutions were used, in which potassium chloride contributed 0.2, 0.7, 0.8, and 0.9, respectively, of the total osmotic concentration. In each of these sets ten combinations of the other three salts were tested. The method of varying the other three salts may be most easily understood by referring to the diagrams of fig. 7. Each of the four triangles (T2, T7, T8, T9) represents one of these four sets. The cultures of the first set (T2) have 0.2, those of the second (T7) have 0.7, those of the third (T8) have 0.8, and those of the fourth (T9) have 0.9 of their total osmotic concentration due to potassium chloride.

In each of the sets the residual osmotic concentration is distributed among the other three salts in the way shown by the distribution of the dots on the diagrams. Thus in triangle 2 the distribution was 0.8 of the total concentration; in triangle 7, 0.3; in triangle 8, 0.2; and in triangle 9, 0.1. Each of the cultures indicated on the triangular diagrams of fig. 7 represents various proportions of monopotassium phosphate, calcium nitrate, and magnesium sulphate, the amount of potassium chloride being indicated by the number of the triangle. Thus the cul-

tures in each set may be regarded as comprising a series of three-salt solutions similar to the series employed by Shive. The diagram (T0) of fig. 7 represents Shive's series, consisting of

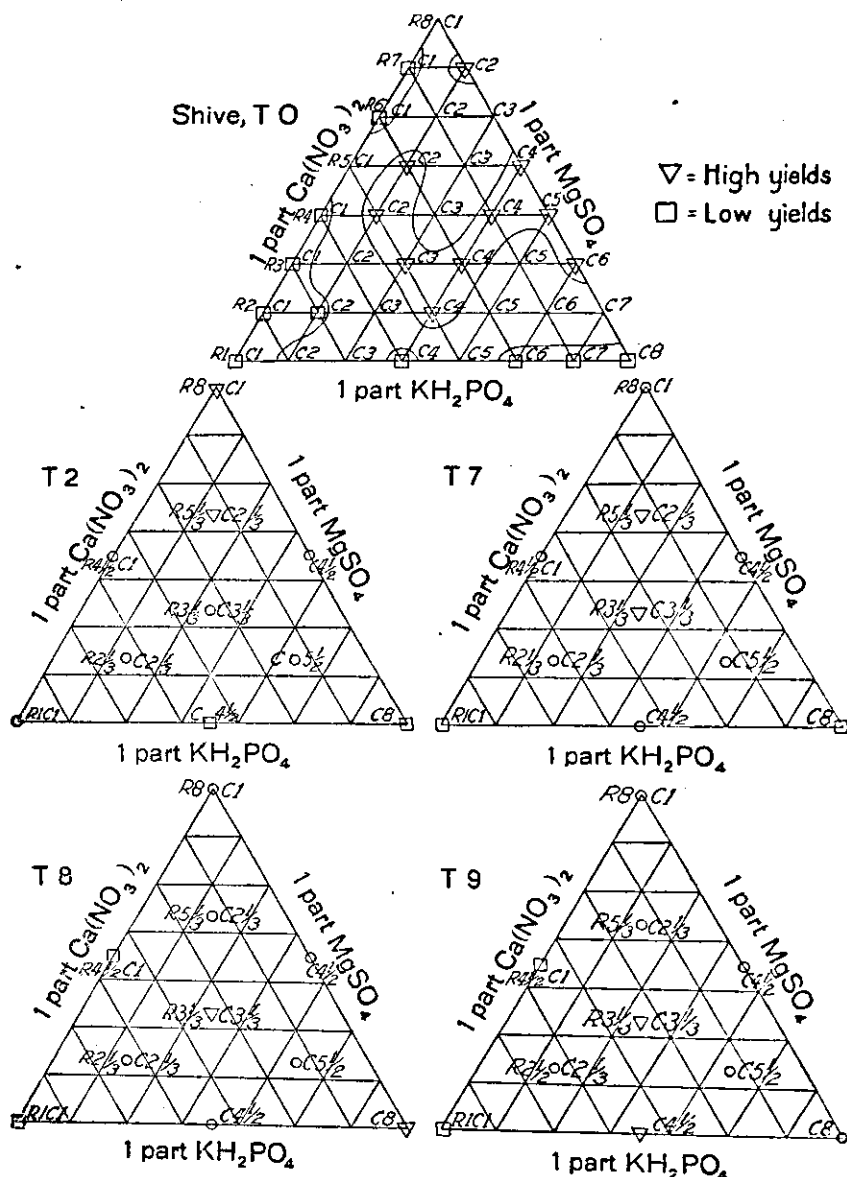


FIG. 7. Diagram for series III, showing culture numbers and osmotic proportions of the four salts.

thirty-six solutions having various proportions of monopotassium phosphate, calcium nitrate, and magnesium sulphate, all of which have the same total concentration (1.75 atmospheres). None of these solutions contains any potassium chloride at all. The set of cultures represented by triangle 2 may be considered as derived from Shive's series by first decreasing the total concentration of the latter to 1.28 atmospheres and then adding to each solution enough potassium chloride to give a total concentration of 1.60 atmospheres. Similarly, the sets represented by triangles 7, 8, and 9 may be derived from the Shive set by decreasing the total concentration to 0.48 atmosphere, 0.32 atmosphere, and 0.16 atmosphere, respectively, and then adding potassium chloride equivalent to 1.12 atmospheres, 1.28 atmospheres, and 1.44 atmospheres, respectively. It is thus seen that series III was planned to study the various physiological values (as indicated by the plants) of the different salt proportions in the Shive series, in the presence of four different partial concentrations of potassium chloride, the total concentration of the four-salt mixture being always the same (1.60 atmospheres).

The actual salt proportions tested in this series were not exactly the same as those employed by Shive, but the total range of salt proportions was the same. Instead of the thirty-six solutions tested by Shive, ten selected solutions were here employed. Only three of these ten correspond to sets of proportions actually used by Shive (those represented by the three apices of the diagram). The others fall on the diagram at different points from those actually tested by Shive, but they may be designated in the same general manner as was followed by Shive, by employing fractional numerals somewhat as in the case of series II. Culture T2R4 $\frac{1}{2}$ C1, for example, considered as a three-salt solution having an osmotic value of 1.28 atmospheres has 0.4 $\frac{1}{2}$ due to monopotassium phosphate, 0.1 due to calcium nitrate, and 0.4 $\frac{1}{2}$ due to magnesium sulphate, and the amount of potassium chloride present is shown by the number of the triangle (0.2 of 1.60=0.32 atmosphere). Besides the forty solutions belonging to this series, solution T2R4C2 (giving the highest top yield in series I) was also employed, for the sake of comparison.

Table 11 gives the chemical composition of each of the forty solutions in series III, in terms of the partial volume-molecular concentrations of the four salts; the values of the three cation ratios are also included in this table. The method used in cal-

culating these partial concentrations was similar to that employed heretofore.

TABLE 11.—Partial concentrations of each of the salts in the solutions employed in series III; also, the values of the three cation ratios; total osmotic value of each solution, 1.60 atmospheres.

Culture No.	Volume-molecular partial concentration.				Cation-ratio value.		
	KCl.	KH ₂ PO ₄ .	Ca(NO ₃) ₂ .	Mg/SO ₄ .	Mg/Ca.	Mg/K.	Ca/K.
	<i>M.</i>	<i>M.</i>	<i>M.</i>	<i>M.</i>			
T2R1C1	0.0067	0.0028	0.0020	0.0280	14.00	2.95	0.21
T2R1C4 $\frac{1}{2}$	0.0067	0.0028	0.0090	.0158	1.76	1.66	0.95
T2R1C8	0.0067	0.0028	0.0161	0.0035	0.22	0.37	1.69
T2R2 $\frac{1}{2}$ C2 $\frac{1}{2}$	0.0067	0.0065	0.0047	0.0187	3.98	1.42	0.86
T2R2 $\frac{1}{2}$ C5 $\frac{1}{2}$	0.0067	0.0065	0.0107	0.0082	0.77	0.62	0.81
T2R3 $\frac{1}{2}$ C3 $\frac{1}{2}$	0.0067	0.0093	0.0067	0.0117	1.75	0.73	0.42
T2R4 $\frac{1}{2}$ C1	0.0067	0.0125	0.0020	0.0158	7.90	0.82	0.10
T2R4 $\frac{1}{2}$ C4 $\frac{1}{2}$	0.0067	0.0125	0.0090	0.0035	0.39	0.18	0.47
T2R5 $\frac{1}{2}$ C2 $\frac{1}{2}$	0.0067	0.0148	0.0047	0.0082	1.75	0.38	0.22
T2R8C1	0.0067	0.0222	0.0020	0.0035	1.75	0.12	0.07
T7R1C1	0.0240	0.00103	0.00072	0.00983	13.65	0.39	0.03
T7R1C4 $\frac{1}{2}$	0.0240	0.00103	0.00323	0.00553	1.71	0.22	0.13
T7R1C8	0.0240	0.00103	0.00575	0.00123	0.21	0.05	0.23
T7R2 $\frac{1}{2}$ C2 $\frac{1}{2}$	0.0240	0.00240	0.00168	0.00655	3.90	0.25	0.06
T7R2 $\frac{1}{2}$ C5 $\frac{1}{2}$	0.0240	0.00240	0.00383	0.00237	0.75	0.11	0.15
T7R3 $\frac{1}{2}$ C3 $\frac{1}{2}$	0.0240	0.00343	0.00240	0.00410	1.71	0.15	0.09
T7R4 $\frac{1}{2}$ C1	0.0240	0.00464	0.00072	0.00553	7.68	0.19	0.03
T7R4 $\frac{1}{2}$ C4 $\frac{1}{2}$	0.0240	0.00464	0.00323	0.00123	0.38	0.04	0.11
T7R5 $\frac{1}{2}$ C2 $\frac{1}{2}$	0.0240	0.00549	0.00168	0.00237	1.71	0.10	0.06
T7R8C1	0.0240	0.00824	0.00072	0.00123	1.71	0.04	0.02
T8R1C1	0.0275	0.00068	0.00047	0.00639	13.60	0.23	0.02
T8R1C4 $\frac{1}{2}$	0.0275	0.00068	0.00213	0.00359	1.69	0.13	0.08
T8R1C8	0.0275	0.00068	0.00378	0.00080	0.21	0.03	0.13
T8R2 $\frac{1}{2}$ C2 $\frac{1}{2}$	0.0275	0.00159	0.00110	0.00426	3.87	0.15	0.04
T8R2 $\frac{1}{2}$ C5 $\frac{1}{2}$	0.0275	0.00159	0.00252	0.00186	0.74	0.06	0.09
T8R3 $\frac{1}{2}$ C3 $\frac{1}{2}$	0.0275	0.00227	0.00157	0.00266	1.69	0.09	0.05
T8R4 $\frac{1}{2}$ C1	0.0275	0.00307	0.00047	0.00359	7.64	0.12	0.02
T8R4 $\frac{1}{2}$ C4 $\frac{1}{2}$	0.0275	0.00307	0.00213	0.00080	0.38	0.03	0.07
T8R5 $\frac{1}{2}$ C2 $\frac{1}{2}$	0.0275	0.00364	0.00110	0.00186	1.69	0.06	0.04
T8R8C1	0.0275	0.00546	0.00047	0.00080	1.70	0.02	0.01
T9R1C1	0.0310	0.00034	0.00023	0.00305	13.26	0.10	0.01
T9R1C4 $\frac{1}{2}$	0.0310	0.00034	0.00104	0.00172	1.65	0.05	0.03
T9R1C8	0.0310	0.00034	0.00185	0.00038	0.21	0.01	0.06
T9R2 $\frac{1}{2}$ C2 $\frac{1}{2}$	0.0310	0.00078	0.00054	0.00203	3.76	0.06	0.02
T9R2 $\frac{1}{2}$ C5 $\frac{1}{2}$	0.0310	0.00078	0.00123	0.00089	0.72	0.03	0.04
T9R3 $\frac{1}{2}$ C3 $\frac{1}{2}$	0.0310	0.00112	0.00077	0.00127	1.65	0.04	0.02
T9R4 $\frac{1}{2}$ C1	0.0310	0.00151	0.00023	0.00172	7.48	0.05	0.01
T9R4 $\frac{1}{2}$ C4 $\frac{1}{2}$	0.0310	0.00151	0.00104	0.00038	0.37	0.01	0.03
T9R5 $\frac{1}{2}$ C1 $\frac{1}{2}$	0.0310	0.00179	0.00054	0.00089	1.65	0.03	0.02
T9R8C1	0.0310	0.00269	0.00023	0.00038	1.65	0.01	0.01

RESULTS OF SERIES III

Appearance of the plants.—The same kinds of top and root modifications described for series I and II were observed in the present series, with the exception of the longitudinal striping of the leaves and the phenomenon similar to "stooling," which did not appear. Retardation of lateral roots was most pronounced in culture T2R1C1, but it was also severe in cultures T7R1C1, T8R1C1, and T9R1C1. Here also the color of the tops was seen to decrease in intensity in passing from left to right in the triangles; and all of the plants in the cultures of triangle 2 were greener than the plants in the corresponding cultures of triangles 7, 8, and 9. The forms of leaf injury apparently related to high partial concentrations of magnesium sulphate were observed in this series, and their distribution is shown upon the diagrams of fig. 8. In these diagrams the total number of leaves of the twelve plants grown in the duplicate cultures are indicated by the numerals placed near the points showing the location of culture solutions. Cultures marked by triangles showed severe injury; those marked by squares showed slight injury.

Dry weights.—The actual dry weights, in grams, of tops and of roots, are given in Table 12. The dry weights of the plants of each of the two duplicate cultures and the average weights are shown. High yields are indicated in the table by the letter H; and low, by the letter L; the two highest yields in each triangle are considered high and the two lowest are considered low, for tops and for roots. The actual yields obtained at the same time with the T2R4C2 cultures are given at the bottom of the table. The data given in this table are shown diagrammatically in fig. 7 (tops) and fig. 9 (roots). The method of plotting is somewhat different from that previously employed; in this case high values are indicated by small triangles and low values by small squares, no attempt being made to indicate areas of high and low values.

Water absorption.—The data on water absorption for the cultures in this series are shown in Table 13, where the arrangement is similar to that in the preceding table.

Water requirement.—The average amounts of water absorbed per unit of dry weight of tops and of roots are presented in the last two columns in Table 13.

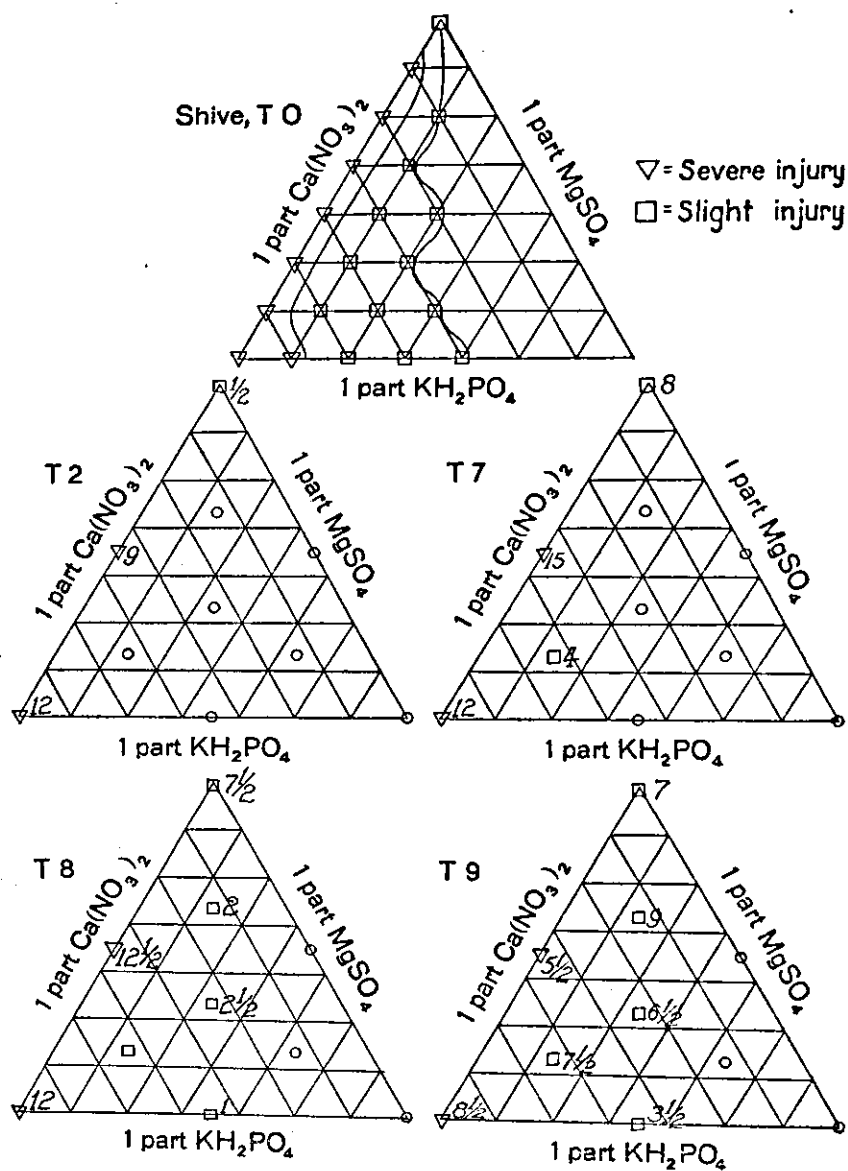


FIG. 8. Diagram for series III, showing leaf injury.

DISCUSSION OF SERIES III

Appearance of plants.—From the data shown in fig. 8, it appears that the area of magnesium injury on the triangular diagram employed for this series is very small when the amount of potassium chloride present is low and becomes larger as the

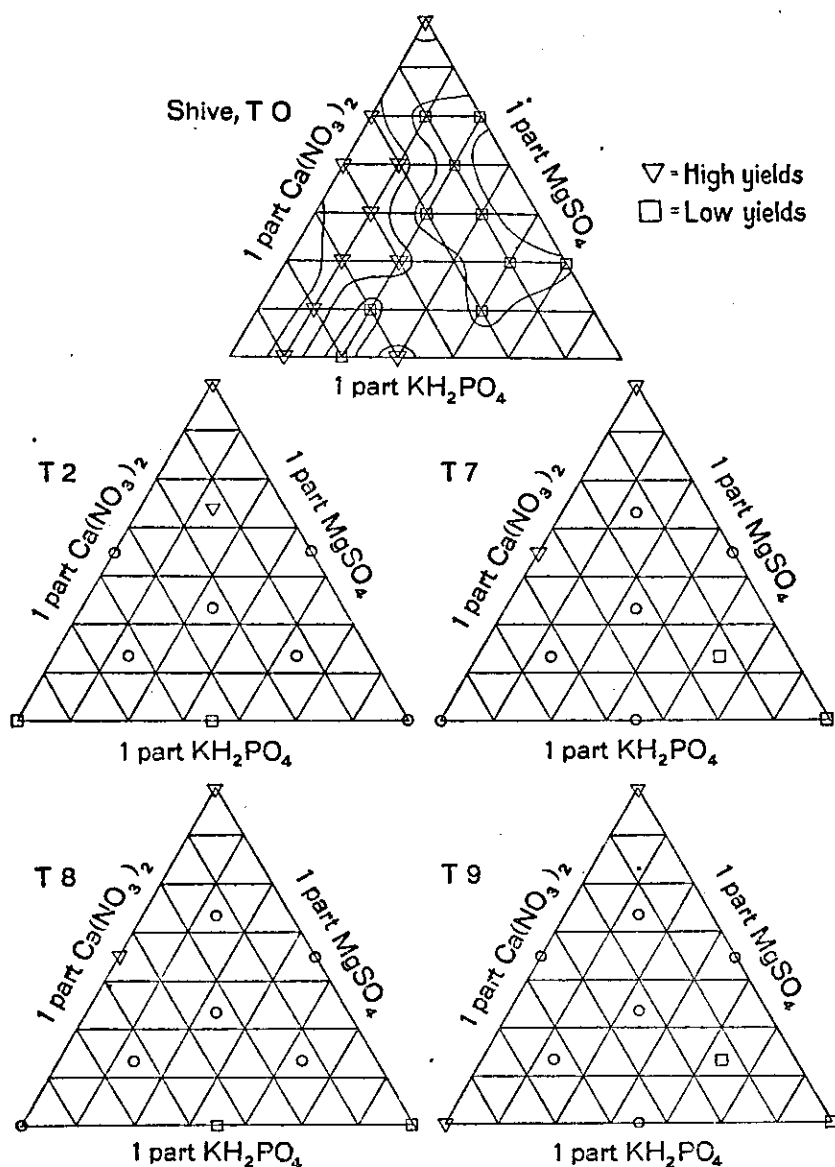


FIG. 9. Diagram for series III, showing dry yields of roots.

amount of this salt is increased. Thus in triangle 2, where only 0.2 of the total concentration is due to potassium chloride, this area of injury is confined to the left margin; it extends somewhat more to the right in triangle 7; and occupies the left half of the diagram in triangles 8 and 9. In the last two cases potassium

chloride was present in very large amounts (0.8 and 0.9 of the total osmotic value, respectively). It is remarkable that the set of cultures represented by triangle 2 is most nearly like the Shive set (which contained no potassium chloride), but that

TABLE 12.—Dry weights of tops and roots of wheat; for series III, conducted from December 4, 1916, to January 5, 1917.

Culture No.	Tops (6 plants).			Roots (6 plants).		
	A.	B.	Average.	A.	B.	Average.
	<i>g.</i>	<i>g.</i>	<i>g.</i>	<i>g.</i>	<i>g.</i>	<i>g.</i>
T2R1C1.....	0.719	0.711	0.715	0.210	0.205	0.208L
T2R1C4.....	0.692	0.685	0.689L	0.197	0.193	0.195L
T2R1C8.....	0.704	0.642	0.673L	0.242	0.209	0.236
T2R2C2.....	0.851	0.825	0.838	0.225	0.221	0.223
T2R2C5.....	0.795	0.773	0.784	0.237	0.217	0.227
T2R3C3.....	0.870	0.842	0.856	0.240	0.221	0.231
T2R4C1.....	0.847	0.878	0.863	0.233	0.223	0.228
T2R4C4.....	0.820	0.857	0.839	0.308	0.278	0.293H
T2R5C2.....	0.955	0.938	0.947H	0.262	0.240	0.251H
T2R8C1.....	0.939	0.872	0.906H	0.256	0.234	0.245
T7R1C1.....	0.466	0.473	0.470L	0.221	0.215	0.218
T7R1C4.....	0.617	0.532	0.575	0.215	0.194	0.206
T7R1C8.....	0.491	0.592	0.542L	0.205	0.177	0.191L
T7R2C2.....	0.585	0.614	0.600	0.215	0.195	0.205
T7R2C5.....	0.585	0.579	0.582	0.201	0.186	0.194L
T7R3C3.....	0.616	0.668	0.637H	0.230	0.219	0.225
T7R4C1.....	0.555	0.531	0.543	0.256	0.216	0.236H
T7R4C4.....	0.625	0.607	0.616	0.212	0.202	0.207
T7R5C2.....	0.656	0.607	0.632H	0.232	0.201	0.217
T7R8C1.....	0.563	0.568	0.566	0.248	0.244	0.246H
T8R1C1.....	0.448	0.435	0.442L	0.234	0.216	0.225
T8R1C4.....	0.470	0.553	0.512	0.203	0.178	0.191L
T8R1C8.....	0.599	0.574	0.587H	0.196	0.186	0.191L
T8R2C2.....	0.474	0.537	0.506	0.217	0.208	0.213
T8R2C5.....	0.504	0.598	0.551	0.209	0.197	0.203
T8R3C3.....	0.620	0.548	0.584H	0.247	0.212	0.230
T8R4C1.....	0.433	0.512	0.473L	0.294	0.229	0.262H
T8R4C4.....	0.510	0.531	0.521	0.207	0.199	0.203
T8R5C2.....	0.594	0.537	0.566	0.235	0.226	0.231
T8R8C1.....	0.492	0.467	0.480	0.263	0.263	0.263H
T9R1C1.....	0.467	0.410	0.439L	0.332	0.316	0.324H
T9R1C4.....	0.541	0.593	0.567H	0.240	0.203	0.222
T9R1C8.....	0.526	0.522	0.524	0.215	0.194	0.205L
T9R2C2.....	0.512	0.502	0.507	0.288	0.255	0.272
T9R2C5.....	0.564	0.496	0.530H	0.223	0.211	0.217L
T9R3C3.....	0.488	0.572	0.530H	0.249	0.221	0.235
T9R4C1.....	0.420	0.417	0.419L	0.301	0.291	0.296
T9R4C4.....	0.480	0.565	0.523	0.229	0.214	0.222
T9R5C2.....	0.512	0.478	0.495	0.280	0.254	0.267
T9R8C1.....	0.440	0.458	0.449	0.316	0.303	0.310H
T2R4C2.....	0.937	0.937	0.937	0.252	0.241	0.247

TABLE 13.—Water-absorption data for wheat; also, average amount of water absorbed for each gram of yield of tops and of roots (water requirement); for series III, conducted from December 4, 1916, to January 5, 1917.

Culture No.	Water-absorption.			Average water requirement.	
	A.	B.	Average.	Tops.	Roots.
	cc.	cc.	cc.	cc. per g.	cc. per g.
T2R1C1	383	363	373	522	1,793
T2R1C4½	409	404	407	591	2,087
T2R1C8	401	389	395	587	1,748
T2R2½C2½	436	436	436	520	1,955
T2R2½C5½	419	409	414	528	1,824
T2R3½C3½	444	399	422	493	1,827
T2R4½C1	425	411	418	484	1,833
T2R4½C4½	432	418	425	507	1,451
T2R5½C2½	442	432	437	461	1,741
T2R8C1	456	435	446	492	1,820
T7R1C1	338	324	331	704	1,513
T7R1C4½	401	376	389	677	1,899
T7R1C8	399	360	380	701	1,990
T7R2½C2½	395	357	376	627	1,834
T7R2½C5½	385	369	377	648	1,948
T7R3½C3½	423	396	410	644	1,822
T7R4½C1	334	327	331	610	1,403
T7R4½C4½	390	381	386	627	1,865
T7R5½C2½	387	378	383	606	1,765
T7R8C1	375	344	360	636	1,463
T8R1C1	333	317	325	735	1,444
T8R1C4½	402	339	371	725	1,942
T8R1C8	387	370	379	646	1,984
T8R2½C3½	369	362	366	723	1,718
T8R2½C5½	386	379	383	695	1,887
T8R3½C3½	395	386	391	670	1,700
T8R4½C1	364	322	343	725	1,309
T8R4½C4½	387	354	371	712	1,828
T8R5½C2½	399	387	393	694	1,701
T8R8C1	351	345	348	725	1,323
T9R1C1	315	314	315	718	972
T9R1C4½	411	365	388	684	1,748
T9R1C8	389	364	377	719	1,839
T9R2½C2½	362	345	354	698	1,301
T9R2½C5½	384	365	375	708	1,728
T9R3½C3½	383	348	366	691	1,557
T9R4½C1	319	303	311	742	1,051
T9R4½C4½	386	340	363	694	1,635
T9R5½C2½	360	337	349	705	1,307
T9R8C1	320	319	320	713	1,032
T2R4C2	441	435	438	467	1,773

triangles 8 and 9 are the ones that approach most nearly to Shive's diagram of magnesium injury. Whether the Shive series containing the three other salts without any potassium chloride might have shown the distribution of this injury recorded by Shive, if it had been carried out simultaneously with these four sets, is of course uncertain.

The more-intense green color that characterized the cultures with a large supply of magnesium sulphate in series I and II was also noted in this series; the region of deepest green occurred at the left margin in the triangle in all four cases. Furthermore, the color intensity of these greenest plants decreased from set to set as the potassium chloride content of the solution increased. As has been mentioned, the high potassium chloride content of these sets was accompanied by lower absolute amounts of the three other salts, so that the last observation may well be related to the small absolute amount of magnesium sulphate present in these solutions. Dwarfing of the root system also occurred in this series with high relative amounts of magnesium sulphate, as has been noted for series I and II, and this dwarfing was much more pronounced with high absolute values of this salt than with lower ones. As has been mentioned, striping of the leaves and "stooling" were not observed in series III.

Dry weights.—Reference to the diagrams of fig. 7 shows that as the partial concentration of potassium chloride is increased, the partial concentration of the other three salts together being correspondingly decreased, the area of high top values migrates downward and to the right; that is, toward lower relative proportions of monopotassium phosphate and higher ones of calcium nitrate. That this migration of the area of high tops is not due merely to decreased partial concentration of monopotassium phosphate, calcium nitrate, and magnesium sulphate is suggested by the fact that a similar decrease in the total concentration of Shive's solution (see Shive's paper, figs. 2 and 3) produced a markedly different change in the configuration of the triangle. The migration of the area in question was from the central to the right central portion; that is, toward higher proportions of calcium nitrate, but not toward lower proportions of monopotassium phosphate. But other evidence from the absolute values presented in Table 12 appears to indicate that the main effect here produced by increasing the partial concentration of potassium chloride is primarily related to the concomitant

decrease in the partial concentration of the three salts used by Shive.

A set of cultures, which may be designated as series III A, was conducted in order to determine whether the low top yields obtained with high proportions of potassium chloride were due to the reduction in concentration of the essential salts or to the high concentration of potassium chloride itself. This series was carried out from January 23 to February 24, 1917. The dry-weight data for this series are shown in Table 14. Four solutions were used in this set. The first of these was the T7R1C1 solution, which was used in series I and II, and which, it will be remembered, has 0.7 of its osmotic concentration due to potassium chloride and 0.1 due to each of the other salts, monopotassium phosphate, calcium nitrate, and magnesium sulphate. This solution contains a very high proportion of potassium chloride. In both series I and series II it produced very low top yields. In the case of the second solution designated [T0R3 $\frac{1}{2}$ C3 $\frac{1}{2}$ (0.48 atmosphere)], the composition was the same as that of the T7R1C1 solution, except that the potassium chloride was omitted. The dry yield of tops produced by this solution was 0.764 gram, while the yield from the T7R1C1 culture was 0.700 gram. It is thus clear that the omission of the potassium chloride did not markedly increase the yield of tops. The next solution [T0R3 $\frac{1}{2}$ C3 $\frac{1}{2}$ (1.60 atmospheres)] was derived from the T7R1C1 solution by the omission of potassium chloride and the addition of sufficient amounts of the other salts to give a total concentration of 1.60 atmospheres. It will be seen that this solution is similar to the second solution, but that the total concentration is here increased from 0.48 atmosphere to 1.60 atmospheres. The yield from this culture was 1.221 grams. Thus a very marked increase in yield is brought about by increasing the essential salts from the concentration in which they occur in the T7R1C1 solution (0.48 atmosphere) to a total of 1.60 atmospheres. The fourth solution of this set (T10R0C0) was a single-salt solution containing potassium chloride in sufficient amount to give an osmotic concentration of 1.60 atmospheres. The yield from this culture is very low, being only 0.265 gram. From this set of cultures it may be concluded that the very low yields obtained in series I, II, and III with very high proportions of potassium chloride were due principally to the reductions in the amounts of the essential salts and not to any specific effect of the potassium chloride.

TABLE 14.—*Dry weights of wheat tops and roots; for series III A, conducted from January 23 to February 24, 1917.*

Culture No.	Nature of solution.	Dry weights (6 plants).	
		Tops.	Roots.
T7R1C1 (1.60 atmospheres)	0.7 of osmotic concentration due to KCl, 0.1 to each of the other salts.	g.	g.
		0.712	0.269
		0.687	0.255
T0R3½C3½ (0.48 atmosphere)	The T7R1C1 solution with KCl omitted. Equal osmotic concentration of the essential salts.	0.700	0.282
		0.753	0.257
		0.690	0.244
		0.801	0.268
T0R3½C3½ (1.60 atmospheres)	The T7R1C1 solution with KCl omitted and with concentration of other salts to give a total of 1.60 atmospheres.	0.810	0.267
		0.764	0.257
		1.220	0.879
		1.222	0.410
T10R0C0 (1.60 atmospheres)	Single-salt solution with 1.60 atmospheres osmotic concentration due to KCl.	1.221	0.395
		0.258	0.100
		0.272	0.105
		0.265	0.108

Returning to series III, it will be seen that with all of the ten sets of proportions of the salts other than potassium chloride the greatest dry weight of tops was produced in the solution having the least amount of potassium chloride; that is, for each set of proportions the cultures of triangle 2 gave higher yields than did the corresponding cultures of triangles 7, 8, and 9. The weight of tops varied inversely with the proportion of chloride for the following combinations: R1C1, R2½C5½, R3½C3½, R4½C1, R5½C2½, R8C1. These data indicate that (with a given set of proportions of the essential salts) increased proportions of potassium chloride give decreased top production; though, as has been emphasized, this decrease is probably due merely to the accompanying decrease in the amounts of the essential elements.

The highest dry yield of roots was obtained with the greatest partial concentration (that is, in triangle 9) of potassium chloride with the following combinations of the essential salts: R1C1, R1C4½, R2½C2½, R3½C3½, R4½C1, R5½C2½, R8C1. Considering all four triangles, the weight of roots varied directly with the proportion of chloride for the following cultures: R1C1, R4½C1, and R8C1. The combinations which did not give greatest dry weight of roots with the greatest amount of chloride were R1C8, R2½C5½, R4½C4½. These solutions were characterized by the

largest amounts of calcium nitrate and the smallest amounts of magnesium sulphate; that is, by low Mg/Ca values. These results indicate, therefore, that an increased proportion of potassium chloride gives increased root production, except in solutions having very low Mg/Ca values.

SERIES IV

METHODS OF SERIES IV

Series IV lasted thirty-two days, from January 23 to February 24, 1917, the period being of the same length as for series III. The maximum temperature during this period was 29° C. (February 4, 17, 21) and the minimum was 7° C. (February 11). The average daily maximum for the period was 25° C. and the average daily minimum was 13° C. The mean daily evaporation rate from the atmometers was 15.3 cubic centimeters, and the total loss was 491 cubic centimeters.

In this series it was planned to study the effect upon the plants of different total concentrations for the same set of salt proportions. Only three of the eighty-four sets were tested in this way, and with them was tested a three-salt solution, without potassium chloride, having the salt proportions nearly the same as those in Shive's best solution for wheat. For each one of these four sets of salt proportions eight different total concentrations were employed. The three sets of four-salt proportions used were as follows: (1) T7R1C1, which contained the maximum amount of potassium chloride occurring in any of the eighty-four solutions; (2) T1R1C1, which contained the maximum amount of magnesium sulphate present in any of the eighty-four solutions and which also had the poorest physiological balance for dry top yield in these plants; (3) T2R4C2, which had the best physiological balance for dry top yield. The three-salt solution in this series was one that is to be designated as R5C2½ on the Shive diagram.

For each one of these four sets of salt proportions the eight total concentrations tested, expressed in terms of their osmotic values, were as follows: 0.50, 1.00, 1.60, 2.50, 3.50, 4.50, 5.50 and 7.00 atmospheres. It will be noticed that the third one of these concentrations (1.60 atmospheres) is the one employed in all of the preceding series.

The calculations were based upon the data given for series I, and the various concentrations were obtained by first preparing a solution having an assumed osmotic value of 7.00 atmos-

pheres and then diluting this to give the concentrations required. The assumption is here made that the ionization constants for the salts are the same for the lower and higher concentrations as they are for the solution having an osmotic value of 1.60 atmospheres. This method, therefore, is not strictly accurate. The error thus introduced is practically negligible for the solutions having values below 1.60 atmospheres. For the higher concentrations, freezing-point determinations indicated that this error gradually increased with the total concentration until it amounted to about 8 per cent. Thus solution T1R1C1, planned to have an osmotic value of 7.00 atmospheres at 25° C., proved by the freezing-point method to have an actual value corresponding to 6.50 atmospheres at 25° C. Since the purpose of this series was to study only the general relations between the growth of the plants and the total concentration, the error just alluded to may be disregarded.

RESULTS OF SERIES IV

Appearance of the plants.—Most of the morphological modifications of tops and roots noticed in the preceding series were also observed in series IV; but the longitudinal striping of leaves and branching from the base of the stem were not seen in this series. Root development was retarded in the higher concentrations, both primary and secondary roots being thick and short. In the lowest concentrations the roots were long, slender, and flexible in appearance. Roots in the corresponding concentrations of cultures T7R1C1, T2R4C2, and R5C2½ were about equal in development; but those in the T1R1C1 cultures were all greatly retarded. With all of the sets of salt proportions, the greenness of the plants decreased with decrease in concentration of the nutrient solution. The greenest plants were those having the T1R1C1 salt proportions; those in the R5C2½ and T2R4C2 proportions were somewhat lighter in shade, and those in the T7R1C1 proportions were much lighter. Magnesium injury was not observed in any of the T7R1C1 cultures. Only one plant in the R5C2½ cultures showed injury, this occurring in the 5.50-atmosphere concentration. Slight injury was observed in the T2R4C2 cultures in the 5.50-, 4.50-, and 2.50-atmosphere concentrations. Severe injury, with coiling of the leaves, was observed in all concentrations with the T1R1C1 salt proportions, the more severe injury appearing in the higher concentration.

Dry weights.—The actual dry weights of tops and of roots for this series are given in Table 15, the weights of the plants in each of the duplicate cultures and the average weights being shown. The data given in this table have been plotted as graphs in fig. 10. In these graphs abscissas represent concentration, in terms of osmotic pressure in atmospheres, and ordinates represent yields in grams. The heavy line is the graph for the T2R4C2 cultures, the light line for the T1R1C1 cultures, the dotted line for the T7R1C1 cultures, and the broken line for the R5C2½ cultures.

TABLE 15.—*Dry weights of tops and roots of wheat; for series IV, conducted from January 23 to February 24, 1917.*

Culture No.	Osmotic concentration.	Tops (6 plants).			Roots (6 plants).		
		A.	B.	Average.	A.	B.	Average.
	<i>Atm.</i>	<i>g.</i>	<i>g.</i>	<i>g.</i>	<i>g.</i>	<i>g.</i>	<i>g.</i>
T7R1C1	7.0	0.675	0.532	0.629	0.210	0.240	0.225
	5.5	0.723	0.696	0.712	0.230	0.271	0.276
	4.5	0.788	0.750	0.769	0.305	0.301	0.308
	3.5	0.769	0.760	0.765	0.297	0.266	0.282
	2.5	0.767	0.699	0.733	0.271	0.258	0.265
	1.6	0.712	0.687	0.700	0.255	0.269	0.262
	1.0	0.823	0.600	0.714	0.217	0.216	0.217
	0.5	0.613	0.602	0.608	0.226	0.234	0.230
T1R1C1	7.0	0.709	0.705	0.707	0.203	0.166	0.185
	5.5	0.771	0.740	0.756	0.205	0.196	0.201
	4.5	0.823	0.762	0.793	0.230	0.233	0.232
	3.5	0.823	0.771	0.797	0.236	0.249	0.243
	2.5	0.789	0.763	0.776	0.241	0.257	0.249
	1.6	0.747	0.722	0.735	0.257	0.262	0.260
	1.0	0.650	0.611	0.631	0.204	0.208	0.206
	0.5	0.642	0.610	0.626	0.210	0.207	0.209
T2R4C2	7.0	0.776	0.762	0.769	0.271	0.273	0.272
	5.5	0.851	0.790	0.821	0.314	0.297	0.306
	4.5	0.922	0.885	0.904	0.329	0.304	0.317
	3.5	1.056	1.003	1.030	0.371	0.350	0.361
	2.5	1.164	1.070	1.117	0.373	0.356	0.365
	1.6	1.165	1.133	1.152	0.367	0.379	0.373
	1.0	0.994	0.900	0.947	0.305	0.284	0.295
	0.5	0.973	0.878	0.926	0.268	0.332	0.300
R5C2½	7.0	0.723	0.642	0.683	0.226	0.221	0.224
	5.5	0.819	0.752	0.786	0.272	0.266	0.269
	4.5	0.963	0.912	0.933	0.324	0.305	0.315
	3.5	1.016	0.933	0.975	0.304	0.346	0.325
	2.5	1.127	1.123	1.125	0.350	0.388	0.369
	1.6	1.160	1.143	1.152	0.385	0.345	0.365
	1.0	1.013	0.985	0.999	0.314	0.293	0.304
	0.5	0.908	0.875	0.892	0.271	0.274	0.273

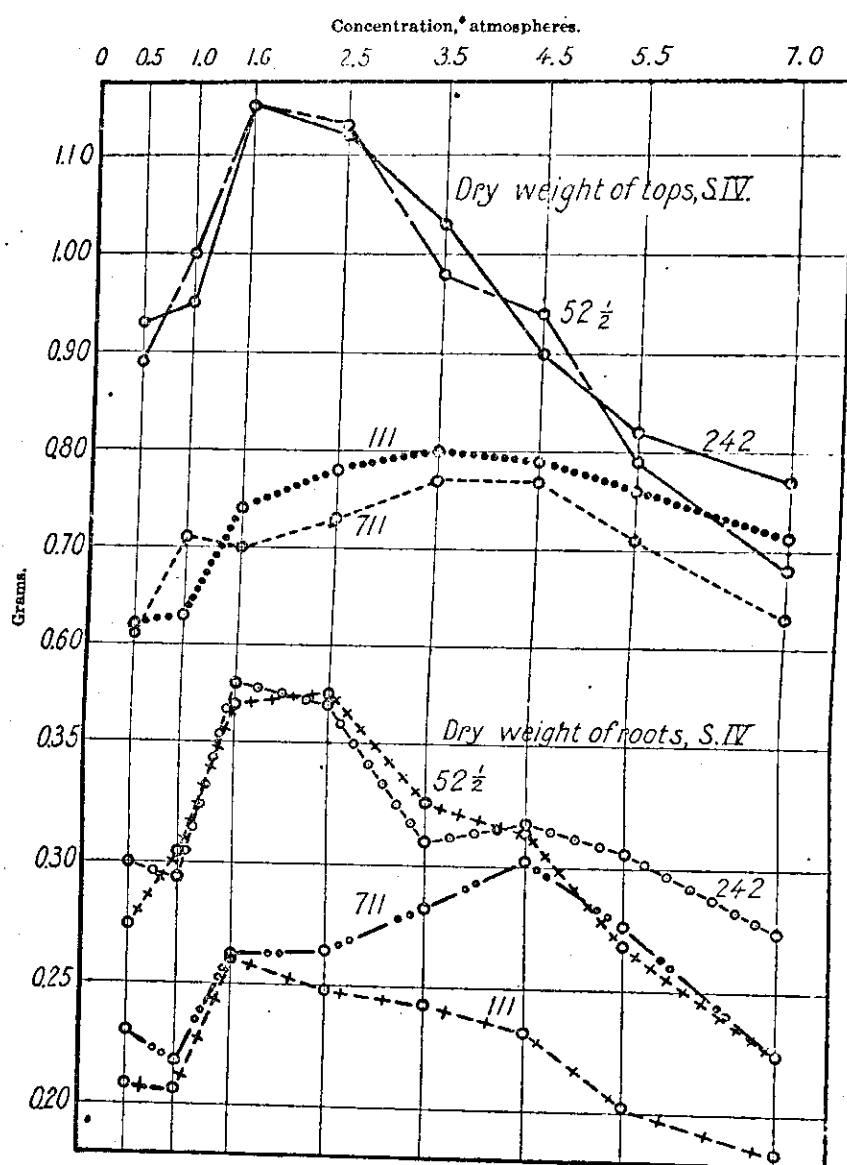


FIG. 10. Graphs of average actual yields (grams) of wheat tops and of roots for series IV.

Water-absorption.—The water-absorption data for this series are shown in Table 16, which corresponds in arrangement to the preceding table. These data have been plotted as graphs in fig. 11, where the method of plotting is similar to that employed in the preceding figure.

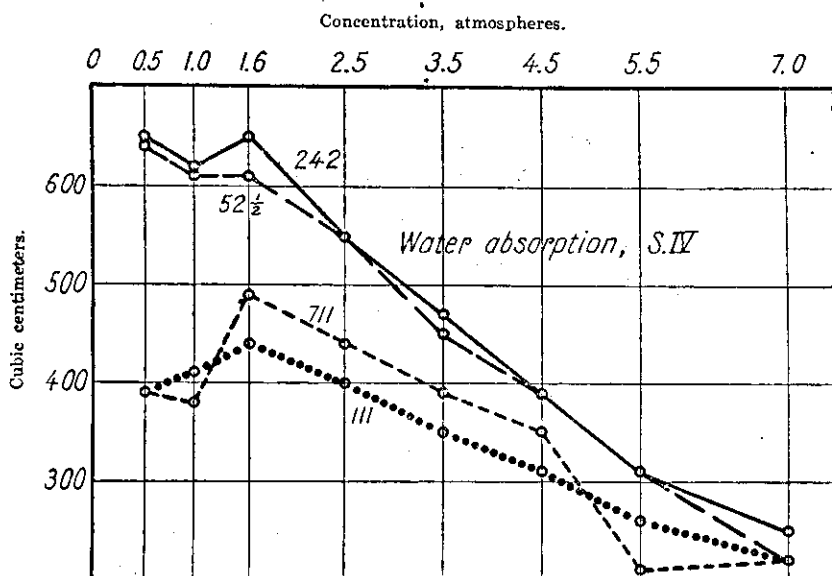


FIG. 11. Graphs of average total amounts of water absorption for series IV.

Water requirement.—The data of the amounts of water absorbed per unit of dry top and dry root yields are shown in Table 16. These data are plotted as graphs in fig. 12, where the method of plotting is similar to that heretofore employed for this series.

DISCUSSION OF SERIES IV

Appearance of plants.—In this incomplete series bearing on the relation of total concentration to the growth of the plants (it being remembered that only three of the many possible sets of salt proportions were tested) there was evidence again that the occurrence of magnesium injury is generally accompanied by a more-intense green color of the foliage. With the set of salt proportions producing greatest injury in a concentration corresponding to 1.60 atmospheres of osmotic pressure (T1R1C1), the severity of the injury as well as the number of leaves injured increased with higher total concentrations and decreased with lower. When salt proportions were employed that gave the highest dry weight with an osmotic value of 1.60 atmospheres (T2R4C2)—which did produce some magnesium injury in series I—no magnesium injury occurred with concentration values below 2.50 atmospheres, though such injury did occur with higher concentration values. The fact that aërial conditions were different from those present for series I may possibly explain why

TABLE 16.—*Water-absorption data for wheat; also, average amount of water absorbed for each gram of yield of tops and of roots (water requirement); for series IV, conducted from January 23 to February 24, 1917.*

Culture No.	Osmotic concentration.	Water absorption.			Water requirement.	
		A.	B.	Average.	Tops.	Roots.
	Atm.	cc.	cc.	cc.	cc. per g.	cc. per g.
T7R1C1	7.0	205	233	219	348	973
	5.5	304	289	297	417	1,076
	4.5	350	311	346	450	1,142
	3.5	406	381	393	514	1,394
	2.5	475	406	441	602	1,664
	1.6	488	487	488	697	1,863
	1.0	404	364	384	538	1,770
	0.5	423	358	391	643	1,700
T1R1C1	7.0	228	215	222	314	1,200
	5.5	261	256	259	343	1,289
	4.5	314	306	310	391	1,356
	3.5	364	339	352	442	1,449
	2.5	405	394	400	516	1,606
	1.6	446	437	442	602	1,700
	1.0	412	398	405	642	1,966
	0.5	396	379	388	620	1,856
T2R4C2	7.0	250	242	246	320	904
	5.5	315	306	311	379	1,016
	4.5	390	381	386	427	1,218
	3.5	489	447	468	454	1,296
	2.5	577	530	554	496	1,518
	1.6	660	632	646	560	1,732
	1.0	638	597	618	652	2,095
	0.5	620	682	651	703	2,170
R5C2	7.0	224	223	224	328	1,000
	5.5	316	305	311	396	1,156
	4.5	402	370	386	412	1,225
	3.5	469	424	447	459	1,375
	2.5	555	536	546	485	1,480
	1.6	617	611	614	533	1,682
	1.0	622	596	609	610	2,003
	0.5	655	620	638	715	2,327

this injury was not apparent with these proportions with a concentration value of 1.60 atmospheres, for which injury was observed in series I. At any rate, these results indicate that magnesium injury is not to be expected with the lower concentrations of this set of salt proportions, but that it is to be expected with higher concentrations. With the other four-salt mixture here tested (T7R1C1, having the highest content of potassium chloride of all the original eighty-four solutions) no magnesium

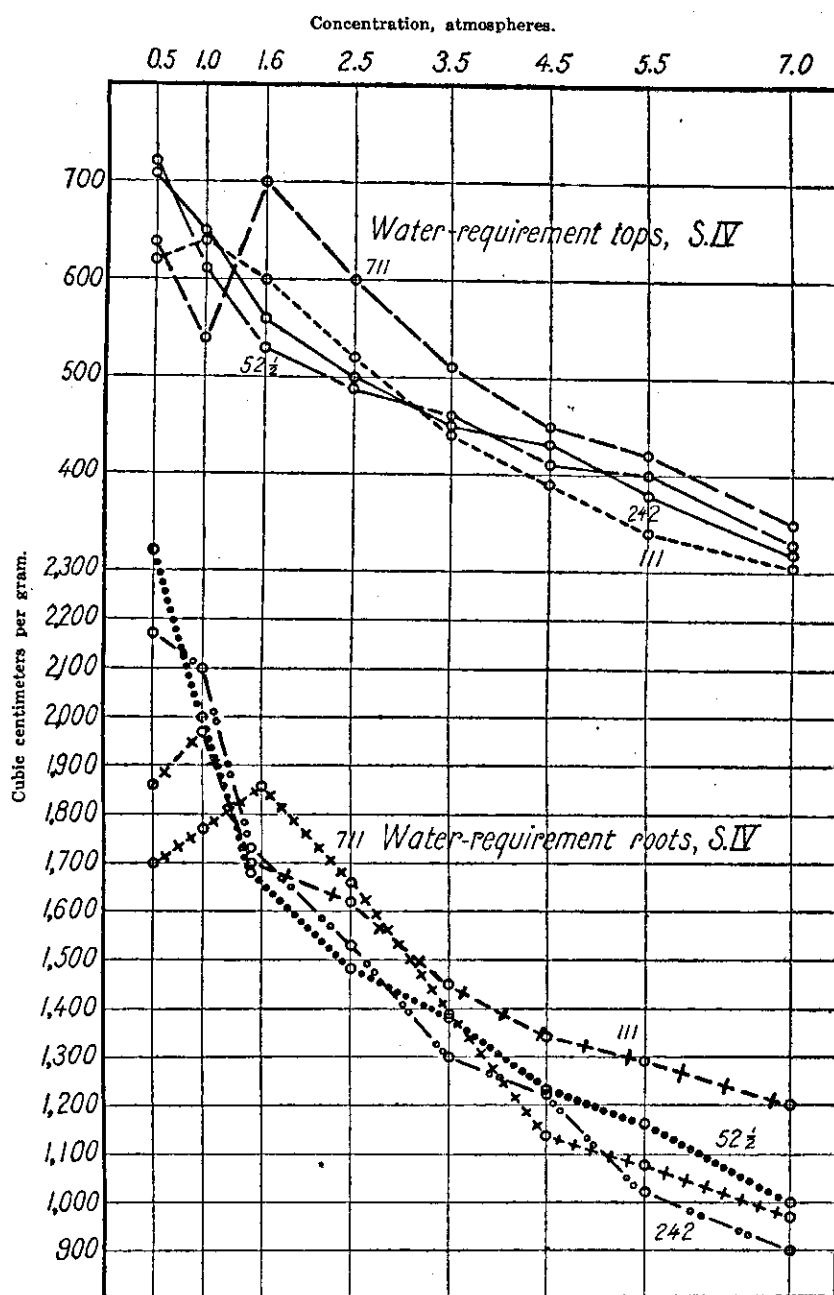


FIG. 12. Graphs of average water requirement of tops and of roots for series IV.

injury occurred, although it did occur in series I with this set of salt proportions for a total concentration corresponding to 1.60 atmospheres. It is clear that magnesium injury does not increase with total concentration with this set of salt proportions. The fourth set of salt proportions tested in this series ($R5C2\frac{1}{2}$ on the Shive diagram, which resembled very closely Shive's best solution) showed no magnesium injury in any of these concentrations, except a slight indication with a concentration value of 5.50 atmospheres, although Shive's best solution regularly produces this form of injury. It is to be noted that while this set of salt proportions differed from that of Shive's best solution to only a small degree, yet this difference was in such a direction as to justify an expectation of less magnesium injury than occurred in the Shive solution. It appears that solution $R5C2\frac{1}{2}$ lies on the border line where more or less marked magnesium injury may or may not occur, according to conditions so far uncontrolled, such as those of the climate or the susceptibility of the individual plants.

Dry weights.—The top yields of this series (fig. 10) bring out what appear to be some very important considerations. With the set of salt proportions ($T2R4C2$) giving highest yields in series I a concentration value of 1.60 atmospheres, or perhaps somewhat higher, appears to be optimal for dry yield of tops. Both lower and higher concentrations give lower yields. With concentrations below this optimum, the yield falls off much more rapidly than with those above. It is especially interesting to note that a total concentration value of 0.50 atmosphere nearly corresponds in top yield with a total concentration value of 4.50 atmospheres. Lower total concentrations than the lowest here employed (0.50 atmosphere) would doubtless have given still lower dry weight values, but it is not to be expected that the latter would have been reduced very much in this way. It is noticeable, on the other hand, that the low top yield occurring with the highest concentration here used (7.00 atmospheres) is much lower than that occurring with a concentration value of 0.50 atmosphere. The three-salt mixture of this series ($R5C2\frac{1}{2}$, on the Shive triangle) agreed very well in all particulars with solution $T2R4C2$. The graph of this set of three-salt proportions may be regarded as indicating what would have been obtained if Shive's set of salt proportions had actually been used. On the basis of this supposition, and on that of the data here given for solution $T2R4C2$, it is not to be expected that either this four-salt solution with chloride, or the Shive three-salt solution

without chloride, can be significantly improved for the production of top yield under these general conditions by altering the total concentration. As has been mentioned, it is possible that the yield might have been a little higher had the total concentration been slightly increased. But it is safe to regard a concentration value of 1.60 or 1.75 atmospheres as optimum for both sets of salt proportions, under the aerial conditions furnished by the greenhouse used in this study, and with the plants and frequency of solution renewal employed.

The two other four-salt proportions included in this series (T1R1C1 and T7R1C1), both of which gave very low top yields with a total concentration value of 1.60 atmospheres in series I and II, here show their highest top yields with a concentration value of 3.50 atmospheres and 4.50 atmospheres, respectively. As in the case just discussed, concentrations below and above the optimum show much lower yields. The two graphs are seen to be nearly parallel throughout. Their form differs from that of the other two graphs of this series, not only in position of the maximum but also in the fact that they are nearly symmetrical about the maximum. Both are rather flat-topped.

While root yields (fig. 10) agree in a general way with top yields as related to the total concentration of the nutrient solution, some rather marked differences occur in other respects. It will be noticed that both the heights of the graphs, indicating actual yields, and the forms of the graphs, showing the relation of changes in concentration to changes in yield, differ for the four sets of salt proportions tested. The graph for the T2R4C2 cultures shows that maximum root yields were obtained with a concentration of 1.60 atmospheres, from which it appears that this solution cannot be significantly improved for root production by changing its total concentration from 1.60 atmospheres. It will be observed, however, that solution R5C2½, which had no chloride and resembled Shive's best solution for tops, gave a slightly higher root yield with a concentration of 2.50 atmospheres than with one of 1.60 atmospheres. The difference, however, is small. With the two concentrations higher than 4.50 atmospheres root yields were significantly higher with the solution containing the chloride (T2R4C2) than with the one that lacked it (R5C2½). Apparently, high total concentrations are less injurious to roots in the presence of the chloride than in its absence. The graph for culture T7R1C1 (having 0.7 of its concentration due to potassium chloride) is

very different in form from those just considered. This graph exhibits a marked maximum at 4.50 atmospheres, instead of at 1.60 or 2.50 atmospheres. The fourth graph, that for the T1R1C1 cultures, having 0.7 of their total concentration due to magnesium sulphate and 0.1 due to each of the other three salts, resembles the first two graphs much more closely than it does the third. With these solutions having very high proportions of magnesium sulphate, the optimum concentration was 1.60 atmospheres, and the yields decreased rather slowly with increasing concentrations above that value. Very high total concentrations retarded root production much less when the solution had high proportions of potassium chloride than when it had high proportions of magnesium sulphate.

This series furnishes very conclusive proof of the point already brought out by Shive and Tottingham; namely, that the optimum total concentration may be expected to vary with the sets of salt proportions used, and that for any total concentration an optimal set of salt proportions may be found. There appears to be no such thing as an optimal total concentration without reference to the salts and salt proportions used, and there is no optimal set of salt proportions except for some specific range of total concentrations.

Water absorption.—The most striking feature of the graphs shown in fig. 11 is the nearly linear decrease in total water absorption with an increase in concentration between the limits 1.60 and 7.00 atmospheres. It will be observed that the graph for the T2R4C2 cultures tends to parallel and lie slightly above that for the R5C2½ cultures. The graph for the T7R1C1 cultures (which have 0.7 of their concentration due to potassium chloride) lies considerably below these two and tends to parallel but remain above that for the T1R1C1 cultures (having 0.7 of their concentration due to magnesium sulphate).

The graphs for the T2R4C2 and the R5C2½ cultures are irregular below 1.60 atmospheres. The R5C2½ cultures, it will be remembered, have no potassium chloride but otherwise are approximately the same in composition as the T2R4C2 ones. It is impossible to determine from these graphs what concentration may be expected to give maximum water absorption, because the values for 0.50, 1.00, and 1.60 atmospheres are so nearly alike. But a markedly lower absorption is evident for concentrations higher than 1.60 atmospheres. Both graphs show an approximately linear decrease in water absorption with an increase in

concentration, between the limits 1.60 and 7.00 atmospheres. The omission of potassium chloride did not alter the relationship between concentration and absorption for concentrations lying between these limits.

The graphs for the T7R1C1 cultures and the T1R1C1 cultures both show perfectly definite maxima at 1.60 atmospheres. Above this concentration, water absorption bears an approximately linear relationship to concentration.

The most interesting portions of all of these graphs are those between the concentrations 1.60 and 7.00 atmospheres. It will be seen that the slopes of the T2R4C2 and R5C2½ graphs are about the same. But the slopes of the T7R1C1 and T1R1C1 graphs are much less steep. Thus changes in concentration in the T7R1C1 and T1R1C1 sets of proportions (both of which were unfavorable media at all concentrations) produced much less marked changes in water absorption than did similar changes in the very favorable T2R4C2 and R5C2½ solutions.

By comparing figs. 10 and 11 it will be seen that for cultures T2R4C2 and R5C2½, between 1.60 and 7.00 atmospheres at least, water absorption is a good measure of top yield, and appears to depend principally upon the size of the plants. But for the T7R1C1 and T1R1C1 cultures, water absorption does not vary in the same way as do top yields. In both of these sets of cultures absorption decreases with increasing concentration between 1.60 and 7.00 atmospheres, while dry weight of tops increases with concentrations of from 1.60 to 3.50 (for T7R1C1) and to 4.50 (for T1R1C1) atmospheres and then decreases. Thus, as the concentration changes from 1.60 to 3.50 or 4.50 atmospheres, top yields increase while water absorption decreases. The difference in amount of water absorbed in this case is not at all a measure of the change in dry weight.

Water requirement.—As shown in fig. 12, a decrease in water requirement of tops accompanies an increase in the concentration of the culture medium. This is true for the T2R4C2 and R5C2½ cultures throughout the whole range of concentrations studied; while for the T1R1C1 cultures it holds only between 1.00 and 7.00 atmospheres, and for the T7R1C1 cultures only between 1.60 and 7.00 atmospheres. This decrease approximates in most cases a straight line; though, for a given change in concentration, there is apparently a more rapid decrease in water requirement with the lower concentrations than with the higher. This is especially marked for the T2R4C2 and R5C2½ cultures, between the concentrations 0.50 and 1.60 atmospheres.

For concentrations above 1.60 atmospheres the T7R1C1 graph lies above the other three for all concentrations. The water requirement for these cultures, which are very high in chloride, is thus higher than for the other three sets for all concentrations between these limits. The graphs for the other three sets of salt proportions lie very close together, and cross one another frequently, so that there appear to be no significant differences between them.

If equal dry weights in different cultures corresponded to equal leaf areas, then the water requirement would of course give an approximate measure of the transpiring power per unit area of leaf surface; that is, of the ability of a unit area of leaf surface to give off water by transpiration.⁵² It is of course not to be expected that equal dry weights do correspond at all rigidly to equal leaf areas, and hence the use of water requirement as a measure of transpiring power would be only a rough approximation at best. But the relations that have been observed in these studies between concentration and water requirement are likely to be approximately the same as those between concentration and transpiring power of unit leaf area. Transpiring power might be expected to decrease, in the way represented by the graphs, with increasing osmotic concentration of the medium surrounding the roots. Transpiring power, for the whole plant, is taken to be practically identical with water-absorbing power, measured by total water absorption.

The graphs for the water requirement of roots (fig. 12) show the same general features as those already described for tops. There is a general decrease in the water requirement of roots with an increase in concentration of the culture medium. The graphs frequently cross, and all have about the same slope, though above 3.50 atmospheres the T1R1C1 graph falls less rapidly than do the others.

The water requirements of roots may be taken as an approximation of the water-absorbing power of the roots per unit root weight and also of their absorbing power per unit area of root surface. This is seen to decrease with an increase in the osmotic concentration of the medium surrounding the roots, as might be expected on physico-chemical grounds.

⁵² Livingston, B. E., The resistance offered by leaves to transpirational water lost, *Plant World* 16 (1913) 1-35. Livingston, B. E., and Hawkins, Lon A., The water-relation between plant and soil, Publication Carnegie Inst. Washington 204 (1915) 5-48.

GENERAL CONCLUSIONS

A mass of experimental data such as is furnished by the present study suggests a very large number of questions and interpretations pertaining to the numerous details of the results. But it is desirable that the first analysis of these results should refer to none but the more broadly general problems. Only these general relations have been included in this study and, of these, those pertaining to the appearance of the plants and the dry yields have received principal attention in this discussion.

It appears that the growth of these wheat plants for twenty-four days was nearly the same, whether a nutrient solution containing (1) Tottigham's four salts, (2) Shive's three salts, or (3) the latter with potassium chloride was employed, provided the set of salt proportions giving the best growth was selected in each case. These three types of solutions appear to have been equally efficient for promoting the growth of the plants. The four-salt solution with potassium chloride apparently offers no advantages or disadvantages, as compared with either of the mixtures previously studied systematically. It was found that the presence of potassium chloride exerted no marked influence, at least for the total concentration principally studied (1.60 atmospheres), when the four salts were used in the proportions giving highest top yields; and the best four-salt solution with potassium chloride contains the other three salts in nearly the same relative proportions as those in which the same salts occur in Shive's best three-salt solution of the same total concentration.

No injurious or retarding effect was observed that could be definitely ascribed to high partial concentrations of potassium chloride, even when this salt made up 0.9 of the osmotic value of the solution; and no characteristic injury was seen that could with certainty be related to the chloride. Retardation of growth associated with high chloride content of the culture solution appeared to be due to the accompanying low concentrations of the other three salts rather than to high partial concentration of the chloride. It is possible that a rather pronounced chlorosis may have been related to a high chloride content of the solution, but the evidence is not definite upon this point.

While it seemed to be impossible to obtain better growth of these plants in the four-salt solution containing potassium chloride than in Shive's best three-salt solution, there is some evidence, nevertheless, that poorly balanced proportions of Shive's three salts may have been improved for the growth of the plants,

especially with reference to root yields, by the addition to the solution of a proper amount of potassium chloride.

Since the wheat plant is not very sensitive to changes in concentration of potassium chloride, the osmotic value of the solution must be changed when potassium chloride is added in large enough amounts to cause a physiological response. If the nutrient solution is to remain the same in total osmotic value, the concentrations of the other three salts must be decreased when potassium chloride is added to give high partial concentrations. It is impossible to decide whether such plant responses as are thus obtained are due to the high partial concentration of the chloride or to the low partial concentrations of the three other salts. This dilemma was always encountered in seeking to obtain evidence on the points just mentioned, and this whole general problem is too complicated to treat experimentally.

It is also difficult to interpret the results in such a way as to determine the action of the chlorine ion (Cl), as such. The problem is complicated by the fact that additions of the chlorine ion to the nutrient solution were always accompanied by equal additions of the potassium ion. It is possible that such additions of the potassium ion may have modified any effects of the chlorine ion that might have been observed under other conditions.

Data on root development are never so easily interpreted as are those on the development of tops in such plants as wheat, a difficulty experienced also in the present study. But effects upon the root system are of especial physiological importance, because this is the part of the plant that is in immediate contact with the culture solution, and it is through the roots that all the water and salts absorbed by the plant must enter. It appears to have been true, in a general way at least, that those salt proportions of the four-salt solution with chloride that gave high top yields also gave high root yields. Conversely, salt proportions giving low top yields generally gave low root yields also. This statement is the opposite of the one given by Shive, based upon his studies with the three-salt solutions. It is possible that the addition of the chlorine ion to the ones already present in the three-salt solution, or some special influence of potassium chloride, may account for this difference. The general indefiniteness, however, of the root data makes superfluous a further discussion of this point without further experimentation.

Certain of the sets of salt proportions with chloride produced a characteristic form of leaf injury, which was observed in

Tottingham's and in Shive's studies, and has been termed "magnesium injury" by Tottingham. The plants giving lowest yields in all three studies exhibited this form of injury, and all three studies support the conclusion that the occurrence and severity of this injury is related to the ionic ratio of magnesium to calcium in the culture solution. This is the only case brought out by any of these three studies (Tottingham's, Shive's, and the present one) in which a clear relation may be regarded as demonstrated between the value of an ionic ratio and the development of the plant. The occurrence of this injury was, in general, not altered by the presence in the solution of potassium chloride, except perhaps with very high proportions of that salt. In the present study the greenness of the foliage was roughly proportional to the severity of the injury, the color being darkest green in the most severely injured plants. Only two sets of salt proportions producing this injury were tested with total concentrations other than the one generally employed in this study; but these agreed in showing that both severity of injury and intensity of color increased with increase in the osmotic value of the solution. The plants in the most dilute solution (0.50 atmosphere) were markedly chlorotic.

The occurrence of magnesium injury is apparently limited, as has been stated, by the value of the Mg/Ca-ratio. With solutions having an osmotic value of 1.60 atmospheres this injury is to be looked for, under the conditions of the present study, when the value of the ratio Mg/Ca is greater than 1.70. Also, the plants may be expected to be without this injury when this ratio value is below 0.80. Since neither Shive nor Tottingham detected any injured plants in their series of lowest concentrations, and since in series IV of the present study injury was found to increase with increase in concentration, it may be expected that these approximate limits will differ with difference in the total concentration.

The solution giving highest top yields with a total osmotic value of 1.60 atmospheres (T2R4C2) contained the four salts in the following partial volume-molecular concentrations: 0.0047 M calcium nitrate, 0.0138 M monopotassium phosphate, 0.0081 M magnesium sulphate, and 0.0067 M potassium chloride. This solution is not very different from what would be obtained by diluting Shive's best solution for wheat to an osmotic value of 1.28 atmospheres, and then adding sufficient potassium chloride to give a partial volume-molecular concentration of this salt of 0.0067 M. Shive's best solution contains the other three

salts in the following partial volume-molecular concentrations: 0.0052 M calcium nitrate, 0.0180 M monopotassium phosphate, and 0.0150 M magnesium sulphate. The two solutions differ in the value of the Mg/Ca-ratio, which in Shive's solution has a value of 2.88, while in the four-salt solution with chlorine it has a value of only 1.72. As would be expected from this difference in the Mg/Ca-ratios, magnesium injury was less pronounced in the four-salt solution than in Shive's best solution. The best solution with chloride for tops has quite different salt proportions from Tottingham's best four-salt solution without chloride, which has potassium nitrate instead of potassium chloride and has a higher partial concentration of calcium nitrate.

The four salts used by Tottingham (potassium nitrate, magnesium sulphate, calcium nitrate, and monopotassium phosphate) are the same as are employed in the solution generally called Knop's solution, and the three salts used by Shive (magnesium sulphate, calcium nitrate, and monopotassium phosphate) are those used in the Birner and Lucanus solution. Likewise, the four salts used in the present study are the same as those of the solution that has come to be known as Detmer's, which contains the four salts in the following volume-molecular proportions: 0.0130 M calcium nitrate, 0.0039 M monopotassium phosphate, 0.0044 M magnesium sulphate, and 0.0072 M potassium chloride. In the case of each of the three solutions, it has been found that the well-known solution could be markedly improved for the growth of wheat by altering the salt proportions. As indicated in the present study, Detmer's solution may be expected to give only about 0.80 as high top yields as does solution T2R4C2. It is important to note that at least thirty out of the eighty-four different sets of salt proportions employed in the first series of this study gave higher yields than the one indicated for the Detmer proportions.

It is worthy of particular attention that, with an osmotic value of 1.60 atmospheres or higher, the Shive three-salt mixture produced magnesium injury when the salt proportions were such as to give the highest yield of tops. This was also true of the four-salt mixture of the present study in the first series; but the solution giving highest top yields did not exhibit this injury in the second series. It has been suggested that increased growth is the first response to agents or circumstances which would prove injuriously toxic in greater concentration or on longer exposure; in other words, that slight poisoning, such as is caused

by magnesium, is essential for the greatest dry weight of tops.⁵³ The problem thus suggested will not be discussed here, but it is important to consider what salt proportions may be expected to give the highest top yields without magnesium injury. The results of the first two series indicate that either solution T3R3C3 or T2R3½C3½ may fulfill these requirements. An examination of Shive's data makes it appear that his solution R7C2, having an osmotic value of 1.75 atmospheres, should produce highest top yield without magnesium injury. The various characteristics of the solutions just mentioned are brought together for comparison in Table 17.

From a study of the osmotic properties of the nutrient solution, as distinguished from its chemical properties, it was found that the optimum concentration for the yield of tops corresponded to an osmotic pressure of about 1.60 atmospheres, at 25° C., when the salt proportions were those of solution T2R4C2. The indications are that for these salt proportions the optimum concentration may be somewhat higher than 1.60 atmospheres, rather than lower. From the results of the present study this statement is true also for a three-salt mixture which would be designated on Shive's composition triangles as R5C2½ and which, therefore, very closely resembles his best three-salt solution for wheat tops.

The optimum concentration was found to be markedly higher for two other sets of salt proportions of the four-salt solution used in this study. The osmotic value was 3.50 atmospheres for solution T1R1C1 and 4.50 atmospheres for solution T7R1C1. These two solutions had salt proportions that gave relatively low top yields, and the yields from their optimal concentrations were very much lower than those obtained from the optimal concentration of solution T2R4C2, which had the best proportions for top yield. It may be tentatively concluded that solution T2R4C2 with an osmotic value of 1.60 atmospheres, or perhaps a little higher, is about the absolute optimum for these four salts, for the frequency of solution renewal and for the plants employed, and for the general greenhouse conditions and length of growing period of the present study.

It seems worth while to lay stress upon some of the prominent considerations that must be constantly borne in mind in trying

⁵³ Free, E. E., and Trelease, S. F., The effects of certain mineral poisons on young wheat plants in three-salt nutrient solutions, Johns Hopkins Circular N. S. No. 3 (March, 1917) 199-201.

TABLE 17.—*Characteristics of the four-salt solution with chloride giving highest yield of tops, and of various other solutions that are of comparative interest.*

Designation of solution.	Salt proportion.										Cation-ratio value.		
	Ca(NO ₃) ₂ per liter.		KH ₂ PO ₄ per liter.		MgSO ₄ per liter.		KCl per liter.		KNO ₃ per liter.		Mg/Ca.	Mg/K.	Ca/K.
	<i>g. mol.</i>	<i>g.</i>	<i>g. mol.</i>	<i>g.</i>	<i>g. mol.</i>	<i>g.</i>	<i>g. mol.</i>	<i>g.</i>	<i>g. mol.</i>	<i>g.</i>			
Four-salt solutions with KCl (1.6 atmospheres):													
Best for wheat tops (T2R4C2).....	0.0047	0.771	0.0138	1.879	0.0081	0.975	0.0067	0.450	-----	-----	1.72	0.40	0.23
Best for wheat tops without magnesium injury, Series I (T3R3C3).....	0.0072	1.181	0.0103	1.402	0.0038	0.457	0.0101	0.753	-----	-----	0.53	0.19	0.35
Series II (T2R3.5C3.5).....	0.0085	1.395	0.0121	1.647	0.0038	0.457	0.0067	0.450	-----	-----	0.45	0.20	0.45
Detmer (T2.16R1.20C5.47).....	0.0130	2.132	0.0039	0.532	0.0044	0.532	0.0072	0.532	-----	-----	0.34	0.40	1.17
Three-salt solutions (1.75 atmospheres) (Shive):													
Best for wheat tops (R5C2).....	0.0052	0.853	0.0180	2.451	0.0150	1.806	-----	-----	-----	-----	2.88	0.83	0.29
Best for wheat tops without magnesium injury (R7C2).....	0.0052	0.853	0.0252	3.431	0.0050	0.602	-----	-----	-----	-----	0.96	0.20	0.20
Four-salt solution (1.75 atmospheres) (Tottingham):													
Best for wheat tops (T3R1C4).....	0.0101	1.657	0.0109	1.484	0.0081	0.975	-----	-----	0.0034	0.0344	0.80	0.57	0.71

to interpret the experimental results furnished by this study. The growth and development of a particular set of culture plants is, of course, controlled by the environment, which comprises a large number of different kinds of effective conditions. An attempt was made in these experiments to control only a small number of the conditions that may influence the plant. Of these effective conditions of the environment, only the initial concentration (osmotic value), the initial salt content of the solution, the frequency of renewal of the latter, and the duration of the experiment were controlled and taken into account. Other conditions that might act upon the plants and might alter the influence of the controlled conditions were allowed to vary as they did in the experiment greenhouse, without being taken into account at all. Among such uncontrolled conditions may be mentioned, for illustration, the temperature of the nutrient solution and of the air around the foliage, the composition of this air, the radiation, etc.

Since it is apparent that no solution remains unaltered after the introduction of the plants, the frequency of renewal of the nutrient solution must be considered a very important environmental condition. It is well known that the absolute plant values may be greatly changed by altering the frequency of renewal of the solution, and with any other frequency of renewal than the one employed in these experiments the comparative results might have been very different from those recorded in this paper. Other changes in the comparative plant values might have been induced by aerating the culture solutions. The temperature of the culture solution also must have an important effect upon the comparative plant values. With other solution temperatures than those employed, the comparative values obtained might have been very different from those that were obtained in these studies.

It appears probable that any given set of solution conditions may produce very different effects upon the plant according to the kinds and intensities of the conditions other than the solution that are effective. If two duplicate series of different sets of salt proportions or of different total concentrations of the nutrient solution were carried out, one with higher air temperature or with more sunshine than the other, it might well happen that the comparative plant values obtained from one series might be very different from those obtained from the other. It seems possible, for example, that lower optimal concentrations might have been obtained in series IV under aerial conditions that favored higher

rates of transpiration. It may be added that the length of the period during which the plants are exposed to the environmental conditions is unquestionably very important in determining the nature of such results as were obtained in the present study. In consequence of these considerations, it is evident that conclusions drawn from this study can be regarded as applicable only for nonsolution conditions that are not greatly different from those encountered in these experiments. As has been mentioned, these conditions were, in a general way, those of a greenhouse in the winter and spring in the temperate region.

Aside from the conditions of environment there is of course another set of conditions that is very influential in determining plant activities. This is the group of internal conditions, which are effective from within the plant body itself. All that can be done toward the control of these internal conditions must be accomplished either by employing for the experiments plants that are as nearly alike internally as possible, or by subjecting the available plants to thoroughly controlled environments for an adequate period to make them alike. In this work, as in most experimentation of this kind, considerable care was exercised to employ plants, for the different cultures of any series, that were very nearly alike in size and general appearance. This method is clearly not entirely satisfactory, but it is about as good as the present state of our knowledge permits. Of course it is evident, just as in the case of the environmental conditions, that the conclusions of this study can be interpreted only with reference to the particular, initial, internal conditions of the plants used. It is not to be expected that the results would have been quite the same if some other species or variety of plant had been used, or if the plants had been introduced into the experiments at a different stage of their development.

While the somewhat complicated considerations just expressed may make such problems as those dealt with in this study seem very difficult, or even practically impossible of solution, from our present point of view, yet, physiological progress seems to lie in the accumulation of such partial answers to these questions as may be obtained experimentally, and in the careful correlation of these partial answers as they become available. It was with this idea in mind that the study here reported was carried out.

ILLUSTRATIONS

FIG. 1. Diagram for series I, showing culture numbers and osmotic proportions of the four salts. Also, showing the relative dry weights of wheat tops; area of low yields (60-77), denoted by small circles; area of high yields (100-87), denoted by small crosses; culture giving lowest yield is marked by a large circle, that giving highest is indicated by a large cross.

2. Diagram for series I, showing leaf injury; cultures marked by crosses showed severe injury; those marked by circles showed slight injury.
3. Diagram for series I, showing relative dry weights of wheat roots; area of low yields (56-69), marked by small circles; area of high yields (100-80), marked by small crosses; culture giving highest yield is marked by a large cross, that giving lowest yield is indicated by a large circle.
4. Diagram for series II, showing culture numbers and osmotic proportions of the four salts. Also, showing relative dry weights of wheat tops; area of low yields (69-77), marked by small circles; area of high yields (100-92), marked by small crosses; culture giving lowest yield is marked by a large circle, that giving highest is indicated by a large cross.
5. Diagram for series II, showing leaf injury; cultures marked by crosses showed severe injury; those marked by circles showed slight injury.
6. Diagram for series II, showing relative dry weights of wheat roots; area of low yields (56-69), marked by small circles; area of high yields (100-80), marked by small crosses; culture giving lowest yield is marked by a large circle, that giving highest yield is indicated by a large cross.
7. Diagram for series III, showing culture numbers and osmotic proportions of the four salts. Also, dry weights of tops; high yields marked by triangles; low yields marked by squares.
8. Diagram for series III, showing leaf injury; cultures marked by triangles showed severe injury; those marked by squares showed slight injury.
9. Diagram for series III, showing dry yields of roots; high yields marked by triangles, low yields marked by squares.
10. Graphs of average actual yields (grams) of wheat tops for series IV. Also, average actual yields (grams) of wheat roots for series IV.
11. Graphs of average total amounts of water absorption (cc.) for series IV.
12. Graphs of average water requirement of tops and of roots, for series IV.

A NEW GENUS OF MYRSINACEAE FROM THE PHILIPPINES

By ELMER D. MERRILL

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AOPIA genus novum

Flores hermaphroditi, 5-meri. Sepala imbricata, usque ad $\frac{1}{2}$ connata, subcoriacea, epunctata. Petala usque ad $\frac{1}{4}$ connata, imbricata, per anthesin patentia, epunctata. Antherae 5, disco petalis adnato insidentes, quam petalis multo breviores, basifixae, rimis longitudinaliter subintrorsae dehiscentes, staminodeis brevibus alternantibus. Ovarium glabrum, ovoideum, 2-loculare, loculis 1-ovulatis, ovulis a basi erectis; stylo cylindrico, brevi. Fructus ellipsoideus, baccatus, breviter mucronatus, 2- vel 1-spermus. Semen ellipsoideum vel plano-convexum, albumine laevi, endocarpio crustaceo. Arbor glabra, epunctata, foliis alternis, integris vel leviter undulatis, petiolatis, glabris, petiolo apice 1- vel 2-appendiculato-glanduloso. Inflorescentiae axillares, paniculatae, multiflorae, flores spicatim dispositae, bracteolatae.

AOPIA MACROCARPA (Elm.) comb. nov.

Discocalyx macrocarpa (Elm.) Leaf. Philip. Bot. 8 (1915) 2781.

The form described by Elmer as *Discocalyx macrocarpa* is represented by three collections from Mount Apo, Davao District, Mindanao, *Elmer 11867, 10660, 10553*, of which two are in flower and one is in fruit. The species occurs in primary forests at altitudes from 750 to 1,100 meters, and is locally known to the Bagobos as *pamaluyan*.

The original description is very long, yet several very important characters are not mentioned, these being the presence of staminodes alternating with the stamens; the 2-celled ovary, each cell with a single basal ovule; and the often 2-seeded fruit. The peculiar appendiculate-glandular petiole character is mentioned although this is not emphasized. At the junction with the lamina each petiole is provided with one, or more usually two,

rather stout, spreading or subappressed, appendaged glands, these often being 1 mm or more in length.

I do not consider that the species can possibly be placed in *Discocalyx*, and it is so anomalous in the Myrsinaceae that I am by no means certain that it really belongs in this family, although in spite of its anomalous characters it seems to be better placed here than in any other group. The entire absence of the punctate glands in the vegetative and floral organs; its 2-celled ovary, each cell with a single basal ovule; its ellipsoid, 2- or, by abortion, 1-seeded fruits; and its appendiculate-glandular petioles are anomalous characters in the Myrsinaceae, while staminodes are rare in the group, being confined to the quite unallied genus *Rapanea*. If it is properly placed in the Myrsinaceae, it is probably as close to *Discocalyx* as to any other proposed genus.

LOW-SUN PHENOMENA IN LUZON

III. MARINE SUNSETS AND THE DURATION OF SUNSET ON MANILA BAY AND THE CHINA SEA

By WILLARD J. FISHER

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In as much as the sun's upper limb might be supposed to descend at end of sunset to the level occupied at beginning by the lower limb, one would expect the duration of sunset over a water horizon to be unaffected by atmospheric refraction. If this were the case, the duration could be computed from Nautical Almanac data, and would depend only on the observer's latitude and altitude, and the declination of the sun. Having accidentally found that the observed duration was in one case greater than the computed by an amount not to be laid to errors of observation, I have been interested to follow the matter further.

In the astronomical triangle PZS , whose sides are complement of latitude $90^\circ - \psi$, complement of declination $90^\circ - \delta$, complement of altitude $90^\circ - h$,

$$\sin h = \sin \psi \sin \delta + \cos \psi \cos \delta \cos P.$$

If in this we take ψ and δ constant and differentiate, we have

$$dP = \frac{-4 \cos h \, dh}{\cos \psi \cos \delta \sin P}.$$

If dh is in arc minutes, the factor 4 gives dP in time seconds. In our problem, dh is the angular diameter of the sun; dP is the duration of sunset; h is the angular elevation of the sun's center at midsunet, and may be got from the height of the eye and horizontal refraction; it is so small that its cosine is nearly equal to 1, and so h need not be known very accurately; P is the sun's hour angle at midsunet, computed from Nautical Almanac data or observed; for all the sunsets observed P is not far from 90° , and its sine is insensitive to small errors; ψ and δ are supposed accurately known.

Table 1, with explanatory notes, shows the results obtained during December, January, and April, 1918, 1919, and 1920, at Manila, at San Fernando, La Union, and in Benguet, computed with four place logarithms.

TABLE 1.

No.	Date.	Duration.			Mirage.	Type.	Contacts.		Remarks.
		Observed.	Computed.	Difference.			1	2	
	1918	<i>Seconds.</i>	<i>Seconds.</i>	<i>Seconds.</i>					
1	Dec. 22	159.8	147.45	+12.4		B			
	1919								
2	Jan.	145.5	146.6	- 1.1	1				
3	Jan. 10	156.5	146.1	+10.4	0	B			Colton phenomena.
4	Jan. 11	164.0	145.7	+18.3		B			
5	Jan. 18	148.0	144.3	+ 3.7					Harbor breakwater as horizon.
6	Jan. 22	147.0	143.6	+ 3.4	0				
7	Jan. 23	146.0	143.4	+ 2.6	0				
8	Jan. 24	169.0	143.2	+25.8	0	B			
9	Jan. 25	163.0	143.0	+20.0	0		1 ?		
10	Jan. 27	153.0	142.4	+10.6	0	B			Colton phenomena.
11	Jan. 29	150.5	141.9	+ 8.6	0	B			Do.
12	Jan. 31	152.0	141.4	+10.6	0	B			Colton phenomena weak.
13	Apr. 16	133.0	134.7	- 1.7	?	A	1 ?		Mount Mirador. Colton phenomena.
14	Apr. 18	136.5	134.8	+ 1.7		A			Mount Mirador. Colton phenomena strong.
15	Apr. 19	136.0	135.0	+ 1.0		?	1 ?		Do.
16	Apr. 20	158.0	134.9	+23.1		?	1 ?		Mount Mirador. Colton phenomena.
17	Apr. 21	136.0	136.2	- 0.2		A		b	San Fernando.
18	Dec. 9	145.8	148.6	- 2.8	0				
19	Dec. 12	147.1	148.9	- 1.8	0	A			
	1920								
20	Jan. 8	159.0	148.5	+10.5	0				Slight rain.
21	Jan. 12	150.2	145.8	+ 4.4	0		a	a	
22	Jan. 18	148.5	144.4	+ 4.1	0	B	a	a	
23	Jan. 20	143.6	144.0	- 0.4	0		a	a	Colton phenomena weak.
24	Jan. 21	141.7	143.9	- 2.2	2	A	b		Colton phenomena marked.
25	Jan. 22	142.3	143.6	- 1.3	0	A	a	a	
26	Jan. 23	143.0	143.4	- 0.4	1	A			
27	Jan. 24	142.9	143.2	- 0.3	0	A		a	
28	Jan. 25	144.1	143.0	+ 1.1	0	A			
29	Jan. 26	143.9	142.9	+ 1.0	0	A		a	
30	Jan. 27	147.1	142.5	+ 4.6	0	B			Colton phenomena marked.
31	Jan. 28	165.2	142.2	+23.0	0	B	a	a	
32	Jan. 29	163.0	142.1	+20.9	0	B			Colton phenomena weak.
33	Jan. 30	145.1	141.8	+ 3.3	0	B			Do.
34	Jan. 31	156.6	141.5	+15.1	0	B	a	a	Colton phenomena moderate.
35	Feb. 1	149.5	141.3	+ 8.2	0	B			
36	Feb. 2	145.4	141.1	+ 4.3	0	B	b		
37	Apr. 2	134.4	134.4	0.0	0	A	a	a	San Fernando Point Lighthouse.
38	Apr. 3				0	A	a	a	San Fernando. Colton phenomena weak.

TABLE 1—Continued.

No.	Date.	Duration.			Mirage.	Type.	Contacts.		Remarks.
		Observed.	Computed.	Difference.			1	2	
	1920	<i>Seconds.</i>	<i>Seconds.</i>	<i>Seconds.</i>					
39	Apr. 4	134.5	134.8	- 0.3	?	A	a	a	Colton phenomena marked.
40	Apr. 5	134.5	134.5	0.0	0	A	a	a	San Fernando. Colton phenomena weak.
41	Apr. 6	134.9	134.6	+ 0.3	0	A	b	b	Colton phenomena?
42	Apr. 24	158.8	136.9	+21.9	?	?	b1?	a	Mount Mirador. Colton phenomena very strong. End a thin blue line.

No. 1 was made with a stopwatch whose rate was unknown; Nos. 2 to 17 were made with the seconds hand of an ordinary watch, whose error was constantly checked by the time ball of the Manila Observatory, and with either a field glass, a galvanometer telescope, or the naked eye, with suitable protection.

When a field glass (a Lemaire 4-power, Galilean) was used with an ordinary watch (Nos. 10 to 17) the left-hand eyepiece was removed and the watch held in front of the left-hand objective, at such a distance that to the left eye the dial, to the right eye the horizon, were both clearly visible. It is difficult to attend to both images at once, but with practice an accuracy of better than a second can be attained.

Nos. 18 to 36 were made with a $\frac{1}{2}$ second stopwatch (works marked Leonidas W. Fy., Switzerland), and a galvanometer telescope with smoked plane spectacle glass covering the objective. This helped greatly in observing lower (first) contact, during the cool months when the sun is very brilliant even near the horizon, but tended slightly to obscure upper (second) contact and so to shorten the observed duration of sunset.

The correction of the stopwatch was found by averaging five runs of 1 hour each, 30 minutes each, 10 minutes each, and 1 minute each (twenty runs in all), and was found to be exactly proportional to the length of the run within limits of starting and stopping errors, and equal to +0.2 sec./min. In all tests and observations initial error (flyback) was allowed for.

Feeling that Nos. 1 to 36 had established the existence of differences between computed and carefully observed durations of sunset, and as I believed that the explanation must lie in peculiarities of atmospheric refraction, the month of April, 1920, was

spent in observing low-sun phenomena at San Fernando Point Lighthouse, La Union, and at Baguio. For sunset observing, with the hope of making approximate determinations of atmospheric refraction at both lower and upper contacts and at stations from sea level to an elevation of more than 2 kilometers, the apparatus taken consisted of a watch with a high-grade Elgin movement, a $\frac{1}{2}$ second stopwatch (works marked Mont Brillant, W. Fy. Switzerland), a 10-power galvanometer telescope with a light camera tripod, aneroid barometer, thermometer, sling psychrometer, etc. The stopwatch had been carefully rated, as had been done with the other one mentioned above; its rate correction was -1.1 sec./min., its flyback correction $+0.1$ second, both constant. This watch was used for Nos. 37 and 42; it balked in the middle of No. 38, and the other sunsets at San Fernando Point Lighthouse, Nos. 39 to 41, were timed with a National Park stopwatch, which the keeper in charge, Mr. Fernando Quintos, kindly allowed me to use. Its correction was found to be $+0.06$ sec./min., constant. I had hoped to use an engineer's Y-level for this work, with a chronometer, but the nonarrival of the chronometer made the Y-level superfluously accurate.

No. 37 was observed with stopwatch and field glass; Nos. 39 to 42 with 10-power galvanometer telescope on tripod, stopwatch, and watch, thus; at lower contact the stopwatch was started, then stopped at an instant known by the watch, started at another known instant, and stopped at upper contact. Thus not only the duration but also the standard time of each contact was determined.

The sun sets at Manila in a water horizon between Corregidor Island and the promontory of Bataan Province, for a few weeks before and after the winter solstice; at other times of the year the sunset is over a land horizon. Before the solstice in 1918 I made no duration observations, not having any idea that they could be of interest; before the solstice of 1919 continued cloudiness made observations at Manila impossible up to December 9, 1919. I was absent from the city during the Christmas recess, when I had hoped to make observations on the duration of sunrise from points on the Pacific shores of Luzon, but again cloudiness prevented.

Nos. 1 to 12 were made on the sea wall along the Cavite Boulevard, Manila, at a point in latitude north $14^{\circ} 34.4'$, longitude east 8 h. 3 m. 55.2 s., by the City Map of the Bureau of Commerce and Industry; Nos. 18 to 36 were made on the sea wall a little farther south, latitude north $14^{\circ} 34.3'$, longitude east 8 h.

3 m. 55.4 s. Depending on the state of the sea, the eye was 3 to 6 feet above actual sea level. For these locations the extremes for duration of sunset, computed from Nautical Almanac data, are approximately .

	Seconds.
Autumnal equinox	132.0
Winter solstice	147.6
Vernal equinox	133.1
Summer solstice	143.0

Nos. 13 to 16 and 42, were made at the Meteorological Observatory, Mount Mirador, Baguio, Benguet, latitude north $16^{\circ} 25'$, longitude east $120^{\circ} 36'$; the elevation of the standard barometer cistern is 1512.5 meters, and this is nearly the height of the eye in observing. At this point, during a large part of the year the sun sets in a sea horizon of the China Sea, beyond the Lingayen Gulf and the land about Cape Bolinao.

No. 17 was made at a point on the beach of San Fernando Harbor, La Union, 270 paces northward of the old pier at the end of Calle Coronel Duvall. Measurements on a Coast Survey chart locate this point in latitude north $16^{\circ} 37.3'$, longitude east $120^{\circ} 18.5'$; height of eye about 5.5 feet. From this point the line of sight at sunset passed over the surf of the south coral reef at the harbor entrance and just cleared San Fernando Point.

Nos. 37 to 41 were made at San Fernando Point Lighthouse, La Union, latitude north $16^{\circ} 37' 02''$, longitude east $120^{\circ} 16' 33''$; No. 37, from the lighthouse balcony, with the eye at about the level of the lamp, 107 feet; the others, on the ground at the base of the tower, with the eye about 84 feet above the level of the sea. The state of the tide was not considered in computing. The horizon is a sea horizon from north to west southwest, where the islands and land of Cape Bolinao are dimly seen.

In the table, the sixth column, headed "Mirage," indicates whether in any direction there was visible the lifting or floating of land on the horizon, called "looming" by some Cape Cod fishermen. At Manila the sandspit of Cavite, Corregidor Island, and the land near Mariveles, in Bataan Province, served as tests; at San Fernando, the coast north and south, but particularly Santiago Island beyond the Lingayen Gulf. 0 means definitely no mirage observable; 1 and 2, definite or very strongly marked mirage; ? means mirage possible but not certain; leaders indicate here, as elsewhere in the table, no record.

Column 7 indicates the type of sunset, A or B, on which see a later paragraph.

Columns 8 and 9 give data about the contact of 1, lower, and 2, upper limb with the horizon; l, indicates a suspicion that the instant recorded was actually a little tardy; a, perfect contact without blurring; b, less perfect but quite definite.

In the column "Remarks," "Colton phenomena," refers to those peculiar deformations of the sun's limb and face which were first accurately recorded by A. L. Colton,¹ whose sunset photographs made in 1893 still adorn the corridors on Mount Hamilton. These deformations are always present as little ripples on the edge, and may be exaggerated into steps, or notches, or incised gashes, or projecting horns, or the disk may even be split or doubled. They are frequently notable at sea level; at Mount Mirador they are sometimes quite wonderful. They deserve photographic record and careful study, as they afford an optical analysis of the atmosphere from sea level to a great height.

In the course of these observations I have distinguished two types of marine sunset, A and B.

Type A occurs always when mirage is perceptible, and sometimes when it is not, and its observed duration was very nearly equal to the computed, and more nearly as practice and experience gave skill in observation; the agreement is best in those cases where an unshaded telescope and a stopwatch were used, as in Nos. 39 to 41. As the descending sun, vertically compressed by astronomical refraction, approaches the sea horizon, a protuberance of more or less flatness grows out below, and almost simultaneously a line of light appears in the sea horizon, which lengthens horizontally and thickens upward till the protuberance and the line join; the moment of this junction I have called lower contact, 1. For about half the duration of sunset the sun presents the appearance of an inverted fish globe, whose mouth rapidly widens to the sun's diameter; from then on the vanishing disk looks like an ellipse much flattened below, and vanishes as a small elliptical spot, at upper contact, 2. This spot does not sink below the horizon; it "goes out."

Type B never occurs simultaneously with a perceptible mirage, and its observed duration was always greater than the computed, by even as much as 20 or 25 seconds. The descending sun flattens below as it approaches the horizon, which is not always easy to see under it, being comparatively dark. The corners of the disk as it passes below the horizon are rounded, instead of projecting

¹ Colton, A. L., *Sunsets at Mt. Hamilton—some curious effects of refraction*, Contributions from the Lick Observatory, No. 5 (1895).

like the rim of a fish globe, until about mid sunset; then the remaining half-disk begins to show a rim, so that it looks for a time not unlike the "tin hat" or trench helmet of the American Expeditionary Force. This flattens down in the middle faster than it shortens horizontally, becomes a line of light, and disappears in dots and dashes among the waves, if the horizon is near. The disappearance is slow, not like the vanishing of the spot at end as in type A.

I have no definite evidence to explain these two types, my attempts to determine refraction not having been successful in enough cases to warrant a conclusion. But as type A is always associated with horizon mirage, if that is observable, it is doubtless due to the same cause, a reversal of the normal gradient of the atmospheric refractive index in the lower layers of the atmosphere. This would explain its peculiarities.

By analogy, type B would be due to an intensification of the normal gradient, in the lower layers of the air. If this were great enough, it would cause light to follow the curve of the ocean surface, so that objects would be visible at distances indefinitely great, or until the light had all gone by absorption. That considerable intensification of the normal gradient occurs is the reason why islands are sometimes visible at unusual distances at sea, as observed from the steamer "Venezuela" in June, 1918, when islands were plainly seen to the north while the ship was in a position between Shimonoseki and Quelpart Islands, and nearing the latter. One of the navigating officers told me that from that or any neighboring position he had never before seen these islands in several voyages. Objects on the shore of Martha's Vineyard are sometimes visible over the curve of the horizon from Woods Hole which usually are entirely invisible; this is generally most marked under the clouds of a retreating northeaster. Such a strengthened gradient would cause a strong flattening of the sun's lower limb, so great that it might become difficult to judge the true moment of contact, and one would probably estimate it in advance of the truth. There would also be a flattening of the upper limb as it approached the ocean surface, producing a "tin-hat" form, and a final vanishing line of light. The observed excessive durations I would, therefore, attribute to hasty judgment of the moment of lower contact; though with the utmost caution I have been unable to shorten these durations. They are certainly not due to carelessness or to inexperience in the use of a stopwatch.

If these hypotheses are true, type A should always be accompanied by abnormally small refractions; type B, by abnormally large.

But No. 42 is explainable by neither hypothesis. It was observed from high level, 1512 meters, the disk was considerably distorted in its descent, there was no material flattening of the disk at lower contact or before, yet the end was a thin blue line. On account of the difficulty of judging the moment of lower contact with a somewhat hazy sea horizon 75 miles away I supposed, till I had computed the duration from the records, that lower contact had been noted too late. Yet the duration came out longer by 21.9 seconds than that computed. The distortion was such as to prevent an assignment to either type.

Diffraction at upper contact has also suggested itself as a plausible cause for a real, not merely an illusory, prolongation of sunset. It could never show itself with a mirage, but a normal or an intensified normal gradient would be favorable. It would cause an apparent increase of refraction at upper contact as compared with lower.

MALAYAN BEES

By T. D. A. COCKERELL

Of the University of Colorado

The bees described or recorded in this paper were all received from Prof. C. F. Baker, to whom we are indebted for greatly increasing our knowledge of the species of Borneo, Singapore, and Penang. As he remarked, these materials are of much interest to any student of the Philippine fauna, because it is not until we know what is found in other Malay regions that we can determine the percentage of really endemic Philippine species or form any distinct idea of the lines of migration which originally populated that area. In other words, the biota of the Malay Archipelago and Peninsula must be studied essentially as a whole, though this is necessarily a vast undertaking, which cannot be completed within the lifetime of present-day workers.

Genus *NOMIA* Latreille

Males, with hind femora greatly enlarged or subglobose. *pachypoda* sp. nov.

Females, or if males, hind femora not greatly enlarged..... 1.

1. Abdomen with green or green and red tegumentary bands; postscutellum unarmed..... 2.

Abdomen without such bands..... 7.

2. Abdomen with only three bands (none on first segment); first two segments metallic; female..... *subpurpurea* sp. nov.

Abdomen with at least four bands (in one Penang male *N. strigata*, the band on first segment has not acquired the green color)..... 3.

3. Legs at least partly red..... *tuberculifrons* Cockerell.

Legs black..... 4.

4. Bands mainly red, with some yellowish green..... *selangorensis* sp. nov.

Bands without red..... 5.

5. Males (Penang, 9610)..... *strigata* (Fabricius).

Females; clypeus keeled..... 6.

6. Abdominal bands with strong lilac tints (Singapore, 9604).

strigata (Fabr.) variety.

Abdominal bands without lilac tints (Singapore, 9606; Penang, 9605).

strigata (Fabricius).

7. Abdomen with white or cream-colored tegumentary bands..... 8.

Abdomen without such bands..... 9.

8. Base of abdomen largely pale red; scutellum dull.

leucozonata penangensis subsp. nov.

Base of abdomen black; scutellum shining..... *perconcinna* Cockerell.

- | | |
|---|---------------------------------|
| 9. Abdomen clavate; males..... | 10. |
| Abdomen not clavate | 11. |
| 10. Abdomen red at base..... | mediorufa morata subsp. nov. |
| Abdomen black at base..... | elongata Friese. |
| 11. Abdomen red at base; females..... | mediorufa morata subsp. nov. |
| Abdomen black at base..... | 12. |
| 12. Scutellum with fulvous tomentum; males.. | scutellata remolita subsp. nov. |
| Scutellum without fulvous tomentum..... | 13. |
| 13. Larger; wings strongly infuscated apically..... | incensa sp. nov. |
| Smaller; wings little darkened apically (Puerto Princesa, Palawan). | palavanica Cockerell. |

Nomia pachypoda sp. nov.

Male.—Length, about 7 millimeters; robust, black with broad abdomen; eyes strongly converging below; tongue long and slender; maxillary palpi with basal joints dark, apical ones pale fulvous; mandibles pale, somewhat reddish; labrum black; face densely covered with ocherous hair; front dull; scape with long outstanding hair; flagellum bright ferruginous beneath; mesothorax, scutellum, and postscutellum densely covered with felt-like fulvous hair; postscutellum unarmed; pleura and metathorax with long ocherous hair; basal area of metathorax very small, minutely granular; tegulae fulvous, rather large but ordinary; wings dusky, stigma (which is small and short) and nervures pale dusky reddish; basal nervure strongly arched; second submarginal cell narrow, receiving the first recurrent nervure beyond the middle; legs mainly black, with pale ocherous hair, but anterior and middle knees, and anterior tibiae at apex, ferruginous; all the tarsi pale yellow, slightly reddish, with the last joint black, abruptly contrasting; hind femora enormously swollen, helmet-shaped, the basal slope above shining, the apex broadly reddish creamy; hind tibiae pallid at base, and gibbous on outer side near base, with a pair of small black tubercles; abdomen finely rugose-punctate; first segment with erect ocherous hair; second and following segments with ocherous hair bands; sixth and seventh appearing entirely pallid; fourth ventral segment broadly emarginate, keeled in the middle.

Singapore (*Baker 9982*), type; also one from Penang (*Baker 9981*).

Nomia subpurpurea sp. nov.

Female.—General appearance and color of abdominal bands (emerald green tinged with vermilion) as in *N. iridescens rhodochlora* Ckll.; first and second abdominal segments metallic as in typical *iridescens*. The face is longer in proportion to its breadth than in true *iridescens*. It is readily known from both *iridescens* proper and *rhodochlora* by the larger, flattened

scutellum, which is entirely dull, with a granular surface. Tegulae fulvous, black in front and narrowly at base. Wings dusky.

Singapore (*Baker*).

Nomia tuberculifrons Cockerell.

Both sexes from Singapore (*Baker*). The male is new; it differs by being less robust; the scape entirely red in front; third and fourth antennal joints conspicuously red; lower half of clypeus ferruginous, shining, with very few punctures, upper half keeled, labrum and mandibles red; hind legs slender and simple, except that the tibiae are broadened apically, and the apical portion is bent or twisted out of a line with the rest. The abdomen has five pale green bands, slightly tinged with red. The nervures are pale fuscous, not black as described for *N. erythropoda*, but in general the description of *erythropoda* agrees well, and it is possible that *tuberculifrons* is *erythropoda*, or a race of it.

Nomia selangorensis sp. nov.

Female.—Length, about 9 millimeters; robust, black, first four abdominal segments with tegumentary bands, which are pale vermilion, with some green, mainly on first segment; hair of cheeks white, of vertex sooty, of face whitish; mandibles black; clypeus strongly keeled, shining on each side of the keel; front dull and minutely granular; flagellum bright ferruginous beneath; mesothorax and scutellum dull and minutely granular; area of metathorax a transverse sulcus crossed by delicate raised lines; hair of mesothorax and scutellum scanty and black, of postscutellum dense and pale ochereous; tubercles fringed with pale ochereous hair; tegulae fulvous, dark in front; wings dusky, stigma and nervures dusky reddish; first recurrent nervure joining the rather broad second submarginal cell not far from end; legs black, with pale hair, tarsi chestnut red apically; hind basitarsi broad, and with fulvous hair on inner side; abdomen polished and shining, with very minute scattered punctures; first segment at sides with erect brownish ochereous hair; the second and third segments have very scanty short dark hair, appearing bare at first sight.

Malay Peninsula, Selangor (*Baker 9612*). From such species as *N. strigata* this is known by the polished abdomen.

Nomia leucozonata penangensis subsp. nov.

Female.—Length, about or nearly 9 millimeters; agreeing in general with the description of *N. leucozonata* Cameron, from

Borneo, but apparently larger, and certainly with less red on abdomen. Cameron's diagnosis is not consistent in all respects with his detailed description. In our insect the first abdominal segment is pale fulvous, with a broad transverse black band, pointed at each end, and not reaching the lateral margins; in the middle, this band is more distant than the equivalence of its width from the hind margin. The second segment is black, with the base pale fulvous, more broadly at sides. The other dorsal segments are black, and 2 to 4 have marginal tegumentary ivory-colored bands. On the ventral side the first two segments are red or fulvous suffused with dusky, and the third fulvous with a transverse black band. Other characters are: Clypeus shining, depressed in middle, its apical margin red; mandibles red subapically; face and front, all except lower part of clypeus, densely covered with very pale ocherous hair, hiding the surface; cheeks with white hair; scape red basally; flagellum red beneath; mesothorax and scutellum dull and appearing bare, with thin, short, pale hair, a few long dark hairs on scutellum; postscutellum densely covered with ocherous-tinted tomentum; base of metathorax with a curved transverse channel, crossed by irregular small plicæ laterally; tegulæ fulvous; wings strongly dusky, with a large subapical cloud; stigma piceous, rather large; nervures fuscous; anterior tibiæ clear fulvous in front, middle tibiæ with fulvous band in front; hind basitarsi broad. The tongue is very long and slender.

Penang (*Baker 9609*).

Nomia perconcinna Cockerell.

Penang (*Baker*). Possibly a distinct race of this Indian species, as it differs from the type by the hind tibiæ being entirely black and the flagellum duskier red beneath. It is allied to *N. albofasciata* Smith, but differs conspicuously in the color of the pubescence.

Nomia elongata Friese.

Penang (*Baker 9611*). This is the real *N. elongata*, agreeing with Friese's description of the ventral surface of abdomen. Except for the ocherous hair of face and abdominal bands, this agrees with Smith's description of *N. clavata*, from Gilolo; but that description could be applied to several species of this type.

Nomia mediorufa morata subsp. nov.

Female.—Length, about 7 millimeters. Differs from typical *N. mediorufa* Ckll., from Formosa, as follows: Flagellum black above except apically; band on second abdominal segment interrupted in middle; first and second abdominal segments red apically, or first all red except lateral subapical dark patches.

Male.—Slender, with clavate abdomen, the first segment entirely red, the second broadly red in middle apically; face densely covered with tawny hair; antennæ very long, flagellum entirely ferruginous beneath; all the tarsi cream-colored more or less tinged with reddish; anterior tibiæ pale ferruginous, as also the other tibiæ at base and apex, and the middle ones largely in front; hind legs slender and simple; wings dusky, with a diffuse apical cloud; stigma and nervures pale brown; stigma large; second submarginal cell receiving first recurrent nervure in middle; second abdominal segment finely but distinctly punctured, and depressed or constricted basally.

Singapore (*Baker*). The type is a female (9983) with broad black band on first abdominal segment. The male is *Baker* 9607.

Nomia scutellata remolita subsp. nov.

Male.—Differs from typical *N. scutellata* Smith by the wings not being clear hyaline. It is very close to *N. ustula* Ckll., but hind trochanters of male are not toothed, the apical lobe of hind tibiæ is dark, the stigma yellowish ferruginous, and the area of metathorax distinctly sculptured, with cross striæ in middle and fine plicæ at sides. It is also near to *N. takauensis* Friese, from Formosa, but differs in the color of the abdominal bands, which are yellowish brown in *takauensis*. It is also very near to *N. philippinensis* (Friese). All these insects form a little group, with representative races or species in different regions, from India and Ceylon to Formosa and the Philippines. In *remolita* the abdominal hair bands are dull white, and the wings are dusky brownish, with a relatively small ferruginous stigma.

Singapore (*Baker* 9608). *Nomia scutellata* was described from the female. Meade-Waldo ascertained that *N. albofimbriata* Cam. was identical, and believed that *N. ustula* Ckll., from Ceylon, was the male.

Nomia incensa sp. nov.

Female.—Near to *N. levicauda* Ckll., but somewhat larger (anterior wing, 7 millimeters long); wings strongly dusky apically; mesothorax conspicuously larger; middle of front entirely dull; second abdominal segment very finely and closely punctured all over, the following segments dull, not polished and shining. The abdomen has a thin ventral scopa of long hairs. The second submarginal cell is large and square, receiving the first recurrent nervure considerably beyond the middle. The hind margins of the abdominal segments are rufous, and have broad ochereous hair bands, broadly interrupted on first segment, more narrowly on second. Venter of abdomen partly fulvous.

Luzon, Montalban (*Baker*).

Halictus semirussatus sp. nov.

Male.—Length, about 8 millimeters; anterior wing, a little over 6; head and thorax black, the mesothorax slightly blue-black; abdomen bright chestnut red, with a basal and two lateral blackish stains on first segment; legs black, with anterior and middle knees, and anterior tibiae in front (except apex) ferruginous, tarsi more or less reddish apically, hind basitarsi pallid at base. Eyes large, submarginate within (inner orbits strongly concave); cheeks and sides of face with white hair; clypeus prominent, apically with a very broad (broadest in middle) creamy-white band, which is strongly and sparsely punctured; labrum cream color; mandibles ferruginous; antennae long, black, the flagellum obscurely brown beneath, not moniliform; front dull, shining at sides; thorax with dull white hair, dense on postscutellum; tubercles prominent and angular, red at apex; mesothorax and scutellum very densely punctured, somewhat glistening; scutellum distinctly bigibbous; area of metathorax very large, strongly defined, shining, with very strongly longitudinal ridges, which are slightly divergent; sides of metathorax very hairy, posterior face sharply defined all round; tegulae castaneous; wings hyaline, dusky at apex; nervures and stigma reddish brown; second submarginal cell square, receiving first recurrent nervure near the end; third submarginal cell unusually short; outer nervures distinct; legs with pale hair, pale golden on inner side of tarsi; abdomen shining, first segment hardly punctured, second duller, with very minute punc-

tures; rather thin pale hair bands at bases of second and following segments; fourth ventral segment with large tufts of yellowish white hair.

Singapore (*Baker 9984*). A very distinct species, perhaps rather approaching *H. cattulus* Vachal (not *catullus*, as Bingham has it), but known by the red abdomen. *Halictus himalayensis* Bingham has the greater part of the abdomen blood-red, and seems to be somewhat related.

Anthophora caldwelli Cockerell.

Malay Peninsula, Selangor (*Baker*), one male. Described from Foochow, China. The specimen is smaller than Chinese males, but the difference is probably not racial.

Coelioxys siamensis Cockerell.

Malay Peninsula, Selangor (*Baker*). Described from Trong, Siam.

Prosopis feai Vachal.

Penang (*Baker*). One female, having the scutellum immaculate, and the apical yellow mark on clypeus obtusely triangular. As at present understood, *P. feai* is quite variable, and with more material it may be possible to distinguish more than one species. Bingham erroneously describes the clypeus of the female as yellow; Vachal indicates that there is only a yellow spot. Bingham's figure also shows the spot.

Prosopis penangensis sp. nov.

Female.—Like the Philippine Islands *P. opacissima* Ckll., but easily known by the polished, shining scutellum, with some very large punctures along the sides. The first abdominal segment is polished and shining, with excessively minute punctures. The yellow clypeal mark is large and oblong, and the lateral marks are broad-cuneiform. The middle and hind basitarsi are yellow but the anterior ones are brown. This is a much smaller species than *P. feai*, with entirely opaque mesothorax. In the Indian fauna it seems nearest to *P. scutula* Vachal, but the nervures are not pale testaceous yellow, and the tegulae are brown with a large yellow spot anteriorly. The yellow band on prothorax is interrupted. The eyes are brown.

Penang (*Baker 9986*).

Nomada dissessa sp. nov.

Female.—Length, about 6 millimeters; ferruginous red, the head and thorax dusky, but the clypeus, supraclypeal area, tubercles and scutellum paler; no yellow anywhere about the insect; face broad; mandibles and labrum simple; antennæ long, scape red, flagellum black with a very obscure reddish tint beneath; third antennal joint long, fourth shorter; mesothorax bare, coarsely punctured, shining beneath the punctures; scutellum bigibbous; pleura and metathorax with conspicuous white hair; tegulæ bright ferruginous; wings hyaline, faintly dusky, more so at apex; nervures and stigma dark rufo-fuscous; only two submarginal cells, basal nervure going basad of transverse median; second recurrent nervure joining second (morphologically second + third) submarginal cell a considerable distance from its end; legs red, hind tarsi darker; abdomen shining red, hind margins of first four segments broadly and conspicuously dusky; first segment with two large triangular dark areas; segments 2 to 4 each with lateral patches of glittering white hair, only seen in a side view of the abdomen.

Luzon, Mount Maquilang (*Baker*). In my table of Philippine *Nomada* this runs straight to *N. palavanica*, a smaller species without dusky bands on abdomen. It really most resembles *N. lusca* Smith, but is not a variation of that with only two submarginal cells, as the mesothorax is more coarsely sculptured, the area of metathorax is more polished posteriorly, and the first recurrent nervure joins the second submarginal cell very much nearer its base.

Nomada polyodonta sp. nov.

Male.—Length, about 6.3 millimeters; head and thorax black, with the following parts ferruginous: Lower margin of clypeus broadly, lower corners of face, labrum, mandibles, upper border of prothorax, tubercles, anterior corners of mesothorax, greater part of pleura (but not bright, and lower part black), scutellum, and postscutellum; front and mesothorax very densely and coarsely punctured; head large, with broad face, which is covered with glittering white hair; scape black, with a bright red spot at base in front, more or less extended as a line upward; flagellum black, chestnut red beneath, the joints conspicuously denticulate; second antennal joint concealed, third about equal with fourth; thorax bare above, pleura and metathorax with rather thin white hair; tegulæ bright fulvo-ferruginous; wings strongly dusky at apex, stigma and nervures piceous; basal

nervure going basad of transverse median; three submarginal cells, second receiving first recurrent nervure a little before its middle; legs mainly black, knees red, anterior and middle femora and tibiæ red in front (middle femora obscurely), anterior tarsi red; hind tibiæ red at apex; abdomen petiolate, narrowed basally, mainly black; first segment reddened on hind margins except in middle; second with a pair of very large subquadrate red patches, widely separated (not closely approaching as in *N. adusta*); fourth segment with a red band, interrupted mesally and laterally; apex light reddish.

Penang (*Baker*). Very like the Indian *N. adusta* Smith, which I have from the Khasia Hills (*Sladen*), but easily known by the denticulate antennæ.

Allodape sauteriella Cockerell, variety *a*.

Female.—Length, about 5 millimeters, distinctly smaller and less robust than typical *A. sauteriella*, from Formosa, but with no other tangible differences. Scape black; basitarsi dark; mesothorax shining; scutellum dull. The face mark has been turned bright red by cyanide; it may have been yellower than *sauteriella*.

Penang (*Baker* 9976). This may be separable when the male is known.

Allodape breviceps sp. nov.

Female.—Length, about 5.5 millimeters; similar to *A. sauteriella* var. *a*, but readily distinguishable as follows: Head considerably shorter, the eyes therefore shorter and appearing more bulging; face mark broader, its diameter where constricted in middle greater than a side above the constriction; scape cream-color in front; tarsi entirely cream-color; first recurrent nervure joining second submarginal cell much more distant from base; basal half of abdomen obscure brown. The constriction of the very broad face mark is about the middle, not conspicuously below it as in *A. hewittii sandacanensis* Ckll.

Penang (*Baker*).

Genus CERATINA Latreille

The following key separates a series of specimens before me:

- | | |
|--|------------------|
| Scutellum entirely black (Penang Island, <i>Baker</i>)..... | dentipes Friese. |
| Scutellum at least mainly yellow..... | 1. |
| 1. Postscutellum at least mainly yellow..... | 2. |
| Postscutellum entirely black..... | 3. |
| 2. Face below antennæ nearly all yellow; small (Penang).... | metaria sp. nov. |
| Face below antennæ with two large leg-shaped black marks (Penang). | |
| | bipes sp. nov. |

3. Clypeal yellow band without any distinct median upper lobe (Baguio, Benguet) *bicuneata* Cockerell.
- Clypeal yellow band with a well-developed median upper lobe..... 4.
4. Mesothorax all black (Penang Island, *Baker 9974*).
..... *conscripta* Cockerell.
- Mesothorax with four yellow lines or stripes..... 5.
5. Larger; sixth abdominal segment with a large subquadrate yellow patch, emarginate on each side (Singapore)..... *incerta* Cockerell.
- Smaller; sixth abdominal segment with a yellow band, broadly emarginate in middle above (*Penang, Baker 9975*).... *accusator* Cockerell.

Ceratina metaria sp. nov.

Male.—Length, 4 millimeters or slightly over; rather pale dull yellow, with black markings as follows: H-like mark on face, the crossbar between clypeus and supraclypeal yellow patch; front, vertex, and occiput all black except linear extension of lateral face marks (which are squarely truncate above) a short distance up orbits, and a small mark near top of eye; upper part of cheeks, and posterior portion behind the broad yellow band, black; mesothorax black with four well-defined yellow stripes, which do not reach front or hind margins, though the lateral ones almost touch hind margin; axillæ partly black; area of metathorax and posterior face black; abdomen dark brown at base, and with five black bands, about as broad as the intervals between them, fifth band with a more or less distinct linear interruption. The legs and pleura are entirely yellow. Scape yellow in front; flagellum dark reddish brown beneath; mesothorax highly polished, without evident punctures, its posterior margin dull; tegulæ testaceous; wings hyaline, faintly dusky, stigma and nervures brown; apex of abdomen broadly rounded, without a projecting point.

Penang (*Baker*). Resembles *C. beata* Cam., but smaller, with more yellow on sides of thorax, etc.

Ceratina bipes sp. nov.

Female.—Length, about 7 millimeters; black and yellow. Head black, with yellow marks as follows: Broad band on cheeks, extending to occiput; base of mandible (which is very broad); labrum; reversed T on clypeus, the upper part broad and bulbous; supraclypeal band; two elongate-oval spots in front of ocelli; and lateral face marks extending to vertex, narrowed to a line above, but ending in a round spot. The black areas left on face resemble the front legs of a short-legged dog. Scape slender, with a yellow stripe in front; flagellum very faintly brownish beneath, mesothorax black with four yellow stripes, the lateral

ones very broad, and marginal; broad anterior margin of mesothorax dull and finely punctured, the rest polished and impunctate; scutellum, postscutellum, and axillar spot yellow; metathorax yellow with the basal area black; upper part of prothorax, tubercles, and large irregular area on pleura yellow, the latter with a posterior extension; tegulæ testaceous; wings dusky, especially in region of marginal cell and beyond; stigma and nervures dark brown; anterior legs yellow, the tibiæ dusky beneath, and the coxæ with a broad black band anteriorly; middle femora with apex above and a stripe beneath, and their tibiæ on outer side, yellow; hind legs black, with the coxæ largely pale; first abdominal segment yellow, with large black lateral marks, connected by an irregular band across the middle; the other segments are black and rugose, the hind margins of 2 to 4 with narrow yellowish bands, of 5 with a broad band, emarginate in middle anteriorly; venter with first three segments mainly pale, the others dark.

Penang (*Baker*). Resembles *C. ridleyi* Ckll. and *C. canarensis* Ckll., but smaller, and differing in the markings.

NOTES ON TREMATODES FROM THE PHILIPPINES¹

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ONE PLATE

Through the courtesy of Prof. Frank G. Haughwout I have had an opportunity to examine three flukes from the Philippines which are described in this paper.

Fasciola gigantica Cobbold 1856. Plate 1, figs. 1 and 2.

Fasciola gigantica is a long lanceolate fluke found in the liver of a carabao, *Bubalus bubalus* Linn., killed at Manila. It has a length measurement of 29 to 36 millimeters and a width of about 8 millimeters. Although the sides of the body are almost parallel there is a distinct anterior end in the form of a cone, a characteristic which shows its relationship to *Fasciola hepatica*. The integument is uniformly spinous. In the region of the uterus the body is distended dorsoventrad, but along the margins it is compressed and slightly fluted.

The oral sucker is small (13 millimeters) while the acetabulum, almost within the limits of the anterior cone, is 22 millimeters in diameter. A very small pharynx leads into a typical fascioliform digestive tract. Compared with *F. hepatica* the secondary cæcal branches number almost twice as many and the ultimate pockets are much more numerous. The general type of branching is, however, quite the same in the two species.

The excretory bladder extends antieriad as far as the oötype.

The organs of the genital system offer a ready method of differentiating this species from *Fasciola hepatica*. The testes are confined to the anterior half of the animal. The posterior testis is fairly compact and has five or six main arms. The anterior testis, which lies just in front of its mate, is more elongated and has about eight arms. The ultimate testicular cæca are definitely set off from the tubes which lead out into the vasa efferentia, so that the entire organ has the appearance of berries

¹ Contribution from the department of pathology, Union Medical College, Peking.

united into a compound panicle. Long slender vasa efferentia convey the sperm to the region immediately anterior to the acetabulum, where they unite to form a single vas deferens. Where the short vas deferens enters the cirrus sac it bends to the left and enlarges to form the seminal vesicle. This organ twists on itself and then turns anteriorly to form the penis. The latter is quite muscular and has the shape of a bottle with a long neck. The genital pore lies just behind the pharynx in the median line.

The ovary is composed of numerous branches lying to the left of the oötype. It is relatively small. The vitellaria extend from the region of the acetabulum to the subdistal margin of the worm. The ventral follicles are strictly lateral, but the dorsal portion of the glands extends mesad in the posterior half of the worm. The vitelline ducts are less readily made out than in *Fasciola hepatica*. The transverse duct lies just behind the oötype. At its middle a short duct runs into the latter organ. The uterus coils on itself several times, then crosses over to the acetabulum and reaches the genital pore on the left of the cirrus sac.

The eggs measure 140 to 160 μ by 75 to 90 μ , with an average of 145 μ by 85 μ , as distinguished from the measurements of *Fasciola hepatica* eggs, which have an average of 132 μ by 70 μ .

DISCUSSION

The literature on the genus *Fasciola* is considerable, even when one takes into account only the species closely related to *Fasciola hepatica*. With the removal of the species *magna* to a new genus, *Fascioloides* (Ward 1917:3) (4), one is confronted only with the possible species *F. hepatica*, *F. angusta* Railliet, *F. aegyptiaca* Looss, and *F. gigantica*. A close inspection shows that the latter three species are alike in all respects in which they differ from *F. hepatica*. They are elongated flukes with parallel lateral margins. Their anterior cone is distinct but short. Their testes are richly branched but short and occupy a field much more restricted than those of *F. hepatica*. Ovary and vitellaria are richly branched. The lateral divisions of the gut are more numerous. The acetabulum is relatively large and close to the oral sucker. The cirrus pouch is small and much more contracted than in *F. hepatica*. Moreover the egg measurements are remarkably similar, averaging 147 μ by 82 μ for *F. angusta*, 150 μ by 80 μ for *F. gigantica* of Egypt, and 145 μ by 85 μ for the material which I have studied.

In as far as the present data are concerned there is adequate proof that all of the species of *Fasciola sensu stricto* exclusive of *F. hepatica* belong to the same species, *F. gigantica* Cobbold 1856. With this view Blanchard (1895:733) (1) and Stephens (1916:244) (2) are in accord.

Fasciola gigantica, which has been regarded as a parasite of man, is found in a great variety of ruminants. The present record supports the view that it is more widely distributed than had been previously believed.

Paramphistomum anisocotylea sp. nov. Plate 1, fig. 3.

This new species of amphistome, for which I propose the name *Paramphistomum anisocotylea*, was taken from the same host, *Bubalus bubalus*, from which *Fasciola gigantica* was secured. The fluke is ovoid in shape, measuring 6 to 6.3 millimeters long by 3.5 to 4 millimeters wide. It has a conspicuous acetabulum with a diameter somewhat greater than half the animal's length (3.1 to 3.4 millimeters). The fluke is uniformly aspinose.

The oral sucker with a diameter of 0.85 millimeter is directed anteroventrad. A short pharynx without pockets lies immediately above the oral sucker and leads into a short œsophagus. The cæca are inflated, sausage-shaped pouches, which extend to the mid-region of the acetabulum.

The testes lie in tandem arrangement between the oötype and the metraterm. They are large, subovoid to rhomboid in contour, with small vasa efferentia leading anteriorly toward the genital pore. The ovary is a small oval body situated immediately to the right of the oötype and is connected with the latter by a short oviduct. Vitellaria extend from the region of the oral sucker to the posterior half of the acetabulum. The follicles are large and are spread out in a patelliform pattern. Short vitelline ducts connect these follicles with the oötype. No seminal receptacle has been found, but a Laurer's canal is clearly made out. The oötype is surrounded by a spheroidal mass of shell glands. Leading out of the oötype is a very small uterus, which runs forward to the anterior region of the acetabulum where it enlarges and at the same time begins to coil. After a complicated series of serpentine twists it proceeds to the genital pore.

The matured eggs measure from 140 to 160 μ in length by 70 to 85 μ in width with an average of 150 by 80 μ .

Paramphistomum anisocotylea differs in size, relation of the genital organs, and in other particulars from the previously de-

scribed *Paramphistoma*, but is especially differentiated by the extremely large acetabulum. Perhaps it most nearly approaches *Paramphistomum explanatum*, which species is, however, larger and has heavily lobed testes (Fischöeder 1904:599). (3)

Phagicola pithecophagicola g. et sp. nov. Plate 1, figs. 4 to 6.

This interesting fluke was secured from the intestine of the monkey-eating eagle, *Pithecophaga jefferyi* Grant. A few of the specimens were obtained in a smear prepared by Professor Haughwout from the host soon after death. Others were teased out of a portion of the intestine which had been fixed in Bouin's fluid and preserved in 80 per cent alcohol. The host was determined by Mr. R. C. McGregor, ornithologist of the Bureau of Science, Manila.

Phagicola pithecophagicola is a minute fluke with a pyriform body which is entirely covered with jagged spines. The oral sucker is directed almost entirely forward and has on its inner margin an uninterrupted circlet of twelve blunt spines (Plate 1, fig. 5). The body measures 0.35 millimeter in length by 0.22 millimeter in greatest width. The oral sucker is fairly constant in diameter, averaging $78\ \mu$. The acetabulum, somewhat behind the middle of the body, measures only $47\ \mu$ in diameter. The region of the body between the two suckers is capable of enormous extension as is also the unforked portion of the intestine.

A long prepharynx leads back into the pharynx, an important sphincter $26\ \mu$ in diameter, which lies midway between the oral sucker and the acetabulum. Behind this is a moderately long oesophagus. The caeca extend far laterad, but reach no farther posteriad than the middle of the acetabulum.

The excretory system has a bladder approaching that of the Brachycoeliinae, intermediate between a typical V-type and a typical Y-type. It possesses little or no muscular elements. The collecting tubules of the worm have not been worked out.

The testes are ovoid glands about $70\ \mu$ in greater diameter, slightly oblique in position, considerably postacetabular and usually lying ventral to the vitelline follicles. The cirrus sac is lacking. The seminal vesicle is a flask-shaped organ lying transversely just behind the acetabulum, curving anteriorly on the right side of that organ and proceeding forward as a nonmuscular cirrus tube which coils only slightly as it advances to the genital pore. No prostate glands have been found.

The ovary is situated to the right of the oötype. It is sub-ovoid in outline and appreciably smaller than the testes. The

seminal receptacle is a flask-shaped organ lying in a plane slightly anterior to the ovary. Between it and the oötype rising dorsad, is a small Laurer's canal (Plate 1, fig. 6). A short oviduct can be traced into the oötype. Around the oötype are numerous shell glands. The vitellaria consist of from four to six large follicles on each side of the body, confined to the posterior limit. The uterine mass occupies a major portion of the body posterior to the acetabulum. A single coil on the right side of the acetabulum runs toward the genital pore, which is situated just below the forking of the intestine. The eggs average $21\ \mu$ by $11\ \mu$ in diameter.

DISCUSSION

A close study of *Phagicola pithecophagicola* shows it to belong to a group possessing in part the characters of the Brachycoeliinae, in part those of the Microphallinae, in part those that are unique. It differs from the Brachycoeliinae mainly in the position of the vitellaria, ovary, and testes. It differs from the Microphallinae mainly in the possession of an uninterrupted circlet of blunt spines inserted on the inner margin of the oral sucker. In view of the differences of these fundamental points, critical in the classification of trematodes, it seems wise to recognize this as the representative of a new genus, *Phagicola*, and create for it a new subfamily, Phagicolinae.

Designation of subfamily Phagicolinae.—Minute distomes with spinose body and an uninterrupted circlet of spines on the inner margin of the oral sucker. Cæca short, not surpassing acetabulum. Excretory bladder intermediate in type between a V- and a Y-form. Vitellaria postacetabular, consisting of a few large follicles. Testes unlobed, slightly oblique, far postacetabular. Ovary, seminal receptacle and seminal vesicle postacetabular. Cirrus sac and prostate glands lacking, cirrus tube nonmuscular. Genital pore antacetabular.

Type and sole genus, *Phagicola*.

Type species, *Phagicola pithecophagicola*.

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ILLUSTRATION

PLATE 1

- FIG. 1. *Fasciola gigantica* Cobbold; ventral view; showing details of reproductive organs; $\times 44$.
2. *Fasciola gigantica*; details of seminal vesicle and cirrus organs; $\times 17$.
3. *Paramphistomum anisocotylea* sp. nov.; ventral view; $\times 13$.
4. *Phagicola pithecophagicola* g. et sp. nov.; ventral view; $\times 154$.
5. *Phagicola pithecophagicola*; detail of oral sucker, showing spines; $\times 308$.
6. *Phagicola pithecophagicola*; detail of region of oötype, showing ovary, Laurer's canal, seminal receptacle, proximal end of uterus and vitelline ducts; highly magnified.

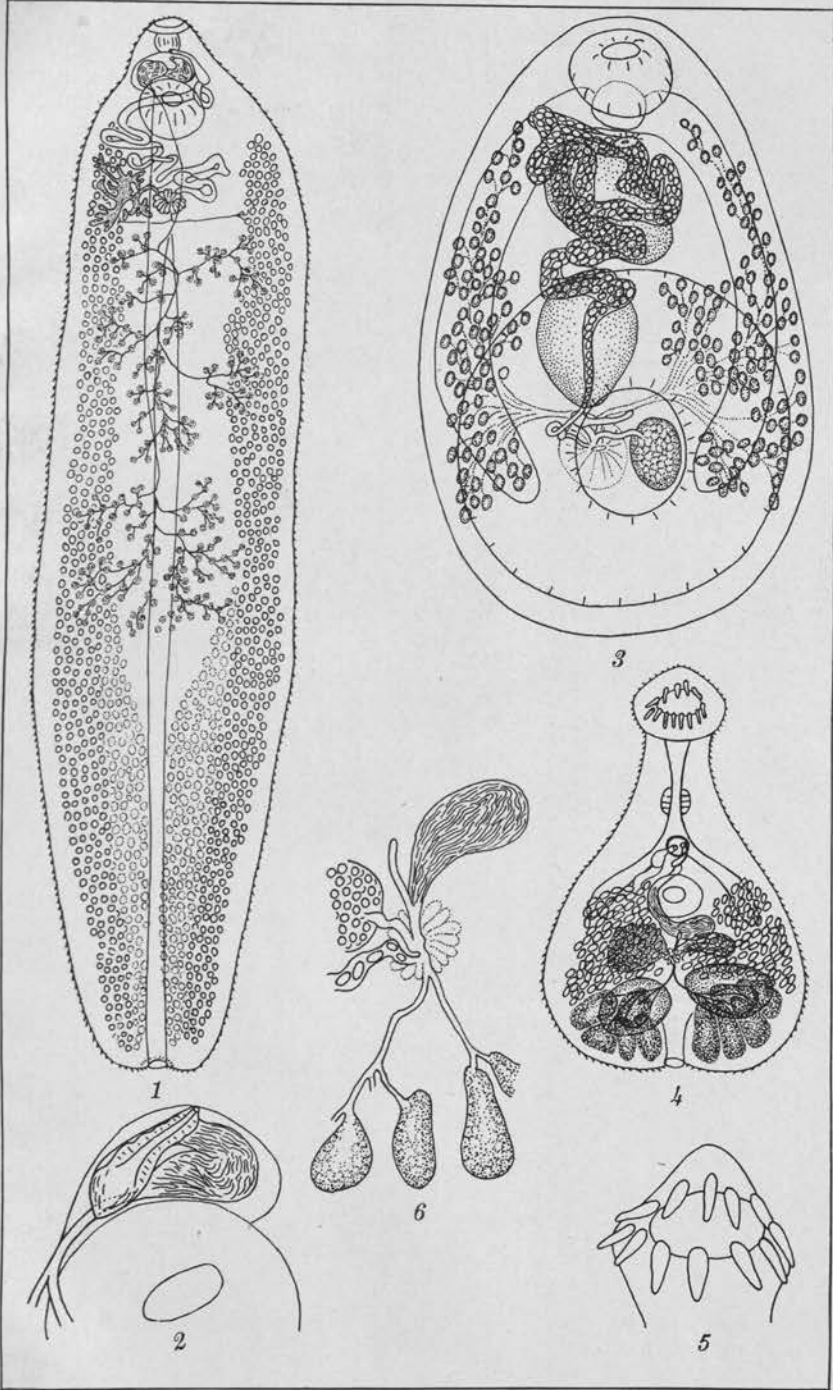


PLATE 1. PHILIPPINE TREMATODES.

BLACK SPOT OF CITRUS FRUITS CAUSED BY PHOMA CITRICARPA McALPINE

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FOUR PLATES

Black spot of citrus fruits was described by McAlpine¹ from Australia, in 1899. McAlpine observed the presence of a fungus uniformly associated with this black spotting and described it as *Phoma citricarpa*, the cause of the disease. No isolations of the fungus or reinoculations are reported in his description. The purpose of the present paper is to present data of such isolation and reinoculation experiments with *Phoma citricarpa* and also to record further knowledge as to the distribution of the disease. In calling attention to the disease and its distribution, it is also hoped that some assistance will be rendered to growers in the citrus-producing countries where it does not yet occur, since with a full knowledge of its characteristics it can be easily excluded. Photographs are presented to facilitate the recognition of the disease.

DESCRIPTION OF THE DISEASE

The spots are found only on the fruits; the leaves and twigs have not been affected, in the experience of the writer. The disease has been observed upon fruits of the sweet orange (*Citrus sinensis*) and the mandarin orange (*Citrus nobilis*). Pummelos (*Citrus maxima*) and calamondins (*Citrus mitis*), although seen in countries where the disease is common, as yet have not been found to be affected. Lemons are reported by McAlpine to be affected. Data are not yet available as to the other species.

Small, reddish-brown spots appear on the surface of the fruit; with increasing age these spots turn darker, becoming sometimes entirely black. The spot may be only 1 or 2 millimeters in diameter, but with time the area may spread to from 7 to 9 millimeters in diameter. As the spot matures a reddish-brown,

¹ McAlpine, D., Fungus diseases of citrus trees in Australia and their treatment. Government Printer, Melbourne (1899) 21, 22, 81.

raised margin forms around the outer edge while the center sometimes becomes depressed, and assumes a light tan or brownish color. Pycnidia sometimes show in the depressed, lighter-colored area; they are black, and a mere fraction of a millimeter in diameter. The lesion not only occurs on the surface but extends into the skin tissue for 1 or as much as 2 millimeters. In this internal tissue the lesion is usually lighter colored—the reddish brown of a young lesion. The lesion has never been observed to extend into the flesh of the fruit, although rarely secondary rots, emanating from a black-spot lesion as the original point of infection, may progress into the flesh. The colored photograph, Plate 1, shows the disease much better than a written description can do.

The disease is not abundant on fruits in the orchard, but seems to develop while they are in storage, or in transit to markets. We have shipped fruits entirely unblemished, which on unpacking one month later were found severely affected by this black spot. The injury to the crop is much the same as that of citrus canker on fruits, and is due to a blemish which lessens its selling value. In a very few cases, the black-spot lesions afford an entrance for rot fungi, but such cases are rare.

DISTRIBUTION

This disease has been observed at Canton, Hongkong, Swatow, Amoy, and Foochow in China. Specimens which emanated from Shanghai have been intercepted by the plant-quarantine inspectors at Nagasaki. Chinese fruits have been collected on the markets in Manila, which were severely affected by this disease, but Philippine-grown fruits have not been observed as yet to be affected. McAlpine, of course, originally reported the disease from New South Wales. The disease has not yet been observed in Japan nor has it been reported from California, Arizona, Florida, or the Gulf States. The distribution on the China coast as far north as Foochow would indicate that the development of the fungus is not limited by the lower temperatures of citrus-growing regions. That is to say, black spot of citrus fruits would seem to be a temperate zone disease.

ISOLATION AND INOCULATION EXPERIMENTS

Isolation experiments were first attempted in Nagasaki, and a fungus was obtained uniformly from such isolations. Sub-

sequently isolations were also made from Chinese fruits found on the Manila markets, and a fungus was isolated which on comparison with cultures from Nagasaki proved to be identical. The fungus answered closely to McAlpine's description of *Phoma citricarpa*.

Inoculation experiments were taken up in Manila; all necessary precautions were taken to maintain such inoculations under quarantine, although the presence of severely affected Chinese fruits in the distant provincial markets were an almost constant source of infection of Philippine-grown fruits had conditions been favorable for infection. The preliminary series of inoculations are here tabulated with the results obtained. The fruits were first disinfected with alcohol, and both control and fungus inoculations were made with needle punctures. All of the fruits were then held in a chamber maintained at laboratory temperatures (from 29° to 32° C.) and with slightly increased atmospheric moisture.

TABLE 1.—*Inoculations on mature Washington navel oranges, with tap water as controls, and with pure culture of Phoma citricarpa.*

[Inoculated April 14, 1920; date of observation of results, May 9, 1920.]

Fruit No.	Punctures per fruit.	Inoculum.	Positive results.
			Per cent.
1	20	Tap water	0
2	20do	0
3	20do	0
4	20	<i>Phoma citricarpa</i> culture.	30
5	20do	70
6	20do	95

The lesions obtained by these inoculations with the fungus were usually dead black in the center, becoming a deep brown at the edges (Plate 2). The fruits could not be held as long as was desirable because of the quick infection with rotting fungi in the warm Manila conditions; fruiting bodies were not found on the surface of the positive cases in the twenty-four days during which the fruits were held. Reisolation, however, on agar plates resulted in the recovery of the fungus in the five cases tried.

Inoculations with the fungus and controls with tap water made at the same time on six similar Washington navel oranges, but

held at a temperature varying closely around 12° C., in all cases were negative. This was attempted for the reason that it was feared that the normal Manila temperatures might be too high for positive infection. The result showed that this was not the case but the instance is presented as of possible value to a future investigator.

Reinoculations were then made on Washington navel oranges. These inoculations were made in two lots; (1) inoculated fruits held in a moist chamber with controls, and (2) fruits held at the normal laboratory atmospheric humidity of Manila in May; the normal humidity in May is not high. The fruits were disinfected with alcohol as previously, and both controls and fungus inoculations were made with needle punctures. The results are shown in Table 2.

TABLE 2.—*Inoculations on mature Washington navel oranges, with tap water for controls, and with pure culture of Phoma citricarpa.*

[Inoculated May 21, 1920; date of observation of results, June 9, 1920.]

Fruit No.	Punctures.	Inoculum.	Conditions of humidity.	Positive results.
				Per cent.
1.....	20	Tap water.....	Dry laboratory...	0
2.....	20	...do.....	...do.....	0
3.....	20	...do.....	...do.....	0
4.....	20	...do.....	Moist chamber...	0
5.....	20	...do.....	...do.....	0
6.....	20	...do.....	...do.....	0
7.....	20	<i>Phoma citricarpa</i> ...	Dry laboratory...	0
8.....	20	...do.....	...do.....	a 65
9.....	20	...do.....	...do.....	a 10
10.....	20	...do.....	Moist chamber...	b 5
11.....	20	...do.....	...do.....	b 25
12.....	20	...do.....	...do.....	b 75

a Doubtful lesions.

b Clearly positive.

Table 2 shows that under dry atmospheric conditions the fungus produces no lesion, or lesions which are very doubtful. With increased atmospheric moisture, 35 per cent of the inoculation punctures were positive; the lesions under such conditions were dead black in the center, becoming slightly reddish toward the margins and varying in diameter from 1 to 3 millimeters. They were in most cases typical black-spot lesions. The fungus was reisolated from the positive lesions. Control punctures with tap water remained entirely negative and in many cases healed so as to be unnoticeable.

Inoculation experiments have been repeated several times since these original results and always, under moderately humid conditions, a reasonable percentage of positive results was produced.

THE FUNGUS IN CULTURE

The fungus grows slowly on the artificial media tried, and is not always easily isolated because of the ease with which secondary fungi may outgrow it. Beef agar + 1, glucose agar + 1, and potato plugs have been used for culturing this fungus; on all of them the fungus makes a restricted growth. The early mycelium is grayish, but the colony soon becomes dead black due to the formation of pycnidia; the colonies are small and restricted (Plates 3 and 4). Pycnidia appear within six or seven days after planting and are abundant, black, spherical, and with pores indistinct.

Under the microscope the young hyphae are hyaline and distantly septate, but with age the hyphae become dark olive brown, closely septate, and twisted and swollen. Spores are borne apically on slender, hyaline conidiophores, and are hyaline, single-celled, smooth and thin-walled, ovate, sometimes becoming almost pyriform, noticeably granular (Plate 4, fig. 2); from cultures they vary in size from 9.25 to 12.25×5.5 to 8.1μ . Spores are not formed profusely. The diagnostic features are the black, carbonaceous, restricted growth in culture and the thin-walled, granular, and somewhat individualistic spores. The best determination of the fungus is its pathogenicity on sweet oranges which may be visible in from fifteen to twenty days. The fungus agrees closely with McAlpine's excellent description of *Phoma citricarpa*, and we consider it identical.

HOSTS

McAlpine describes this black-spot disease on oranges, lemons, and mandarin oranges. The writer's inoculations on lemons in Manila have always resulted negatively; for such experiments mature California lemons were used, probably the Lisbon or Eureka variety or both, purchased in the Manila markets. It may be that these California varieties are not so susceptible as are those grown in Australia. The writer is of the opinion, however, that Manila temperatures are somewhat above the optimum desirable for this fungus, and that inoculations at lower temperatures might produce different results on lemons. Man-

darin oranges have given positive results in Manila; we have no data as yet for other species of *Citrus*.

CONTROL

There are no experimental data regarding control of this disease in an affected orchard. The writer's inoculations have shown that fruits are only susceptible when approaching maturity, while immature fruits give negative results when inoculated. It is possible, therefore, that an easy orchard control, by spraying, could be developed.

For countries where the disease is not yet present, however, as in California, the Gulf States of America, and Japan, the best control is of course entire prevention by excluding the disease. The best of control methods by spraying are not 100 per cent efficient and in addition cause an annual outlay which is repeated year after year. Exclusion of the fungus by the plant-quarantine officers would be 100 per cent control and would cost but a small amount as compared with the yearly outlay for spraying.

The situation in the Philippines with regard to this disease is peculiar. Black-spot disease, as has been said, has not been observed here as yet upon Philippine-grown oranges. Oranges imported from China and found everywhere on the markets are sometimes severely affected with the disease, affording a source of infection of Philippine citrus fruits just at the period when such fruits are ripening. The absence of the disease in the Philippines is therefore probably due to climatic conditions or possibly to the phenomenon that ordinarily the rind of Philippine citrus fruits does not mature and turn yellow, but remains green up to picking time. Since citrus fruits are only susceptible when the rind is well matured, the absence of the disease may be due to the absence of susceptible tissue. This point may be cleared up in future experiments.

SUMMARY

1. Black spot, a disease described by McAlpine from Australia in 1899, has also been observed throughout southern China. It is not yet in Japan or America or in the orchards in the Philippines. The disease consists of a black blemish on the fruits; it is not found on the leaves or branches.

2. The fungus *Phoma citricarpa* McAlpine was isolated from black-spot lesions and, on inoculation upon healthy orange fruits, reproduced the disease. Control punctures remained negative.

The fungus was reisolated in culture from the positive inoculations. Inoculations have since been made a number of times resulting positively in reasonable percentages of cases, indicating that *Phoma citricarpa* is the cause of the black-spot lesions. *Phoma citricarpa* is briefly described from cultures.

3. The sweet orange and mandarin orange fruits were observed to be affected in China. McAlpine also reports lemons to be affected. Other citrus species have not been observed to be affected. The activity of the disease is not limited by the low temperatures of the northernmost citrus-growing regions.

4. Although the disease is not serious and moreover could probably be prevented by spraying methods, it is desirable, in order to avoid the cost of spraying methods, to exclude it entirely from such citrus-growing countries in which it has not yet appeared. The present paper calls attention to the desirability of exclusion for such countries as Japan, California, and Florida.

ILLUSTRATIONS

PLATE 1

Black spot on fruits of Chinese mandarin orange variety. The spots are caused by the fungus *Phoma citricarpa* McAlpine.

PLATE 2

- FIG. 1. Washington navel orange on which twenty needle punctures have been made with tap water.
2. Washington navel orange on which twenty needle punctures were made with an infusion of *Phoma citricarpa*. Both fruits were inoculated at the same time and held under the same conditions.

PLATE 3

- FIG. 1. *Phoma citricarpa* on glucose agar slant, showing black restricted growth; twenty days from planting.
2. *Phoma citricarpa* on potato plug; twenty days from planting.

PLATE 4

- FIG. 1. *Phoma citricarpa* on a plate of standard nutrient beef agar + 1, fourteen days after planting, showing restricted growth; natural size.
2. Conidiophores and conidia of *Phoma citricarpa* McAlpine, $\times 500$.

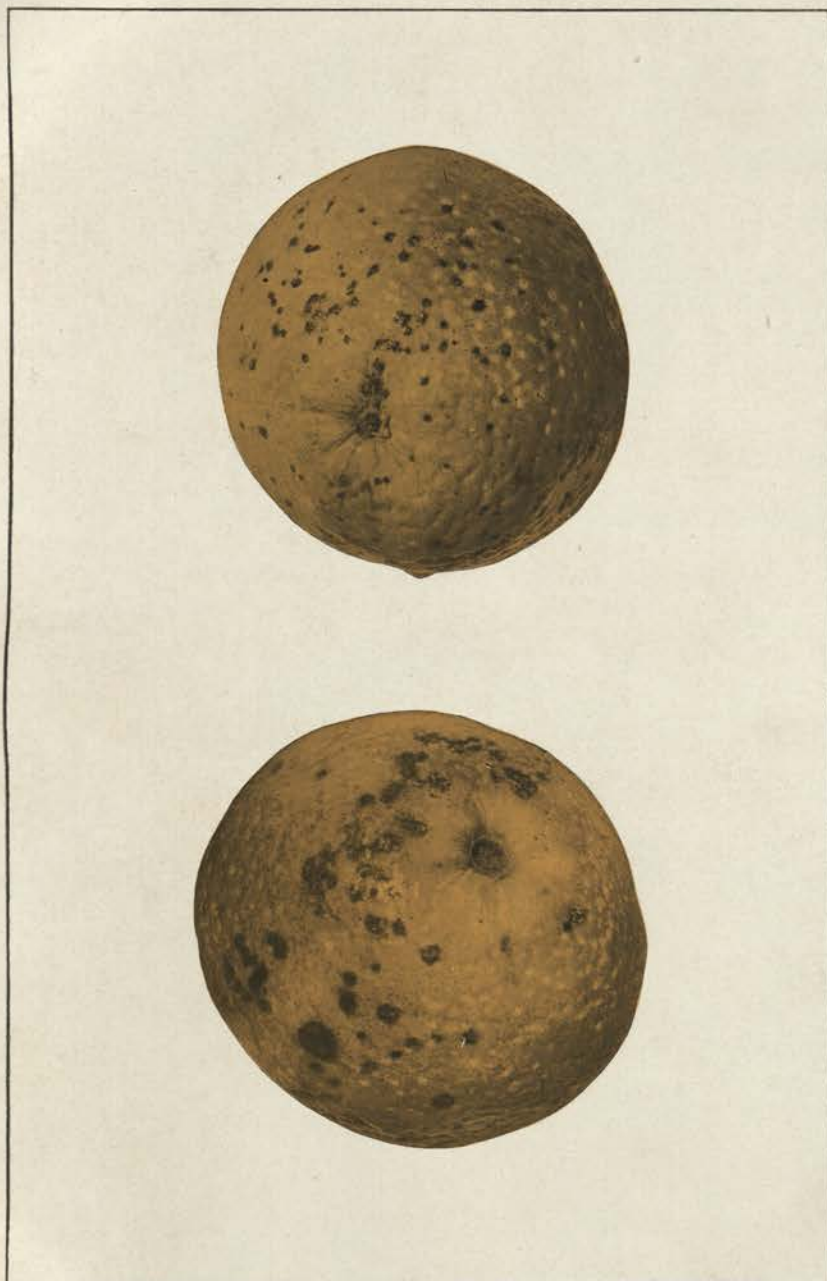


PLATE 1. BLACK SPOT ON FRUITS OF CHINESE MANDARIN ORANGE VARIETY. THE SPOTS ARE CAUSED BY THE FUNGUS *PHOMA CITRICARPA* MCALPINE.

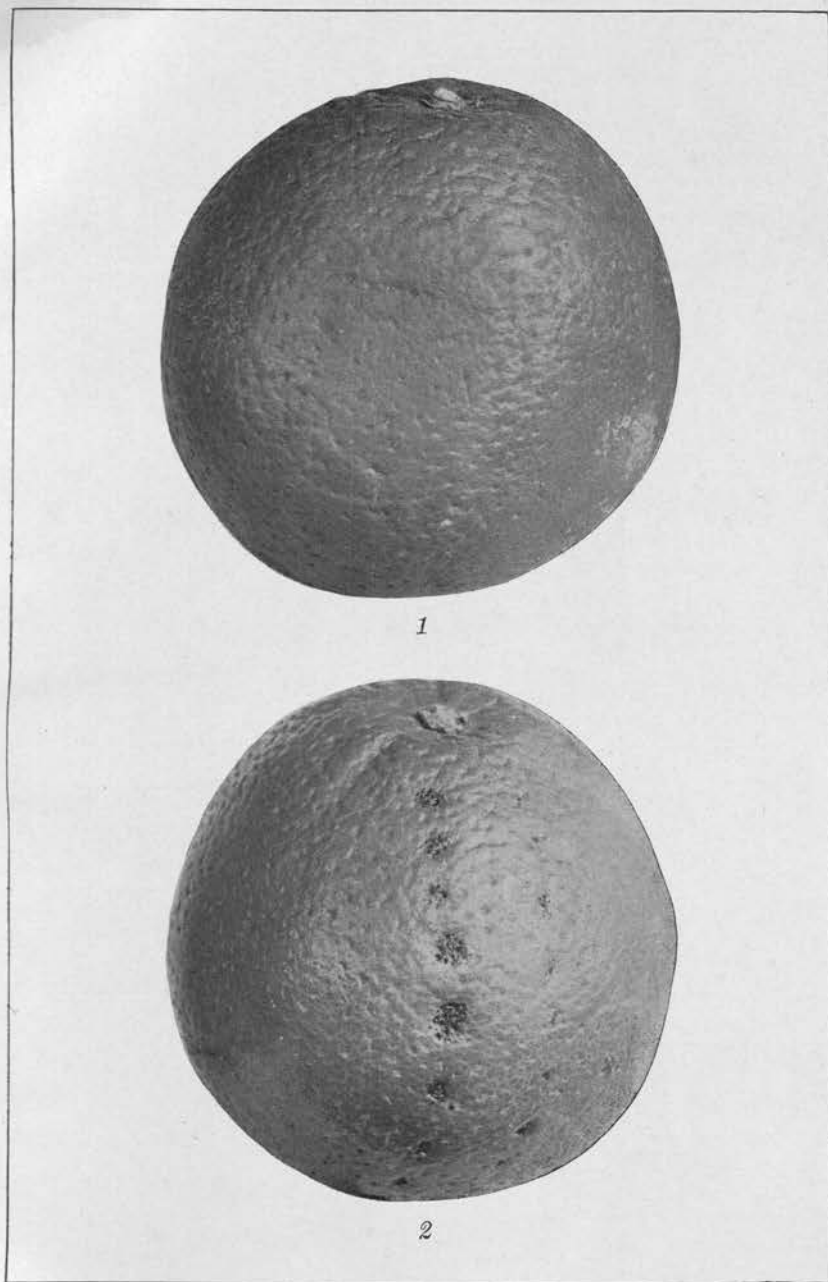


Fig. 1. Washington navel orange on which twenty needle punctures have been made with tap water. 2. Washington navel orange on which twenty needle punctures have been made with an infusion of *Phoma citricarpa*. Both fruits were inoculated at the same time and held under the same conditions.

PLATE 2.

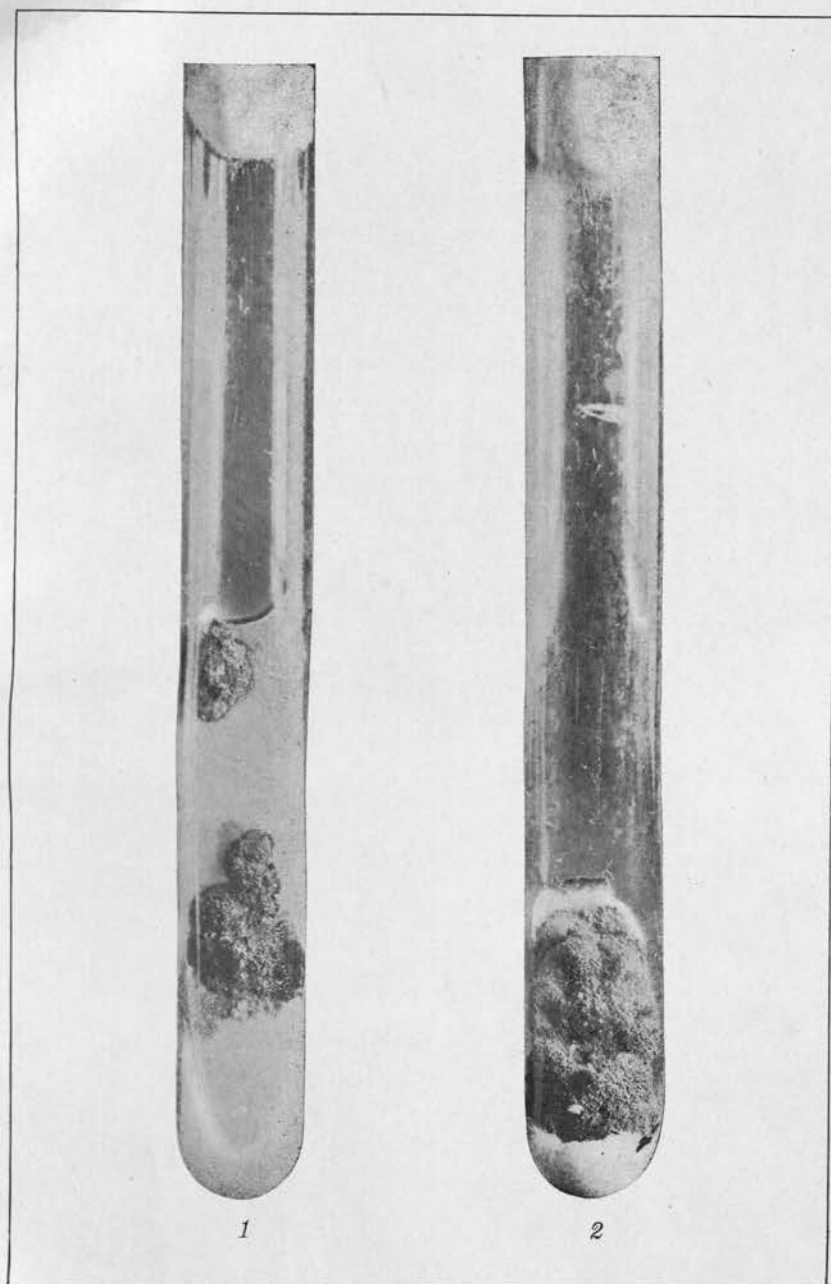


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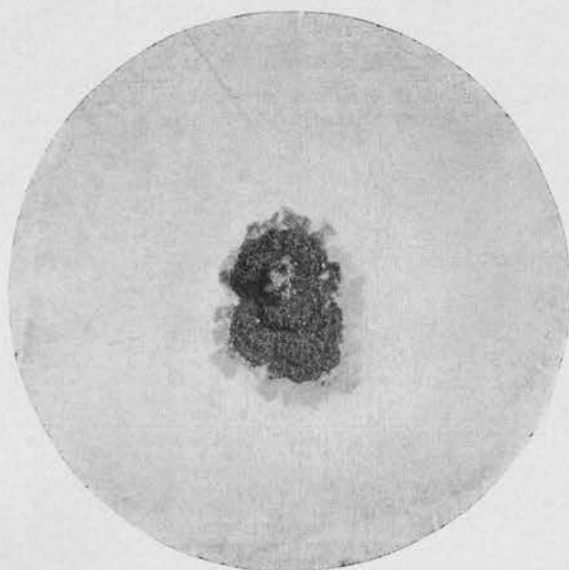


Fig. 1. *Phoma citricarpa* on a plate of standard nutrient beef agar + 1, fourteen days after planting, showing restricted growth; natural size.

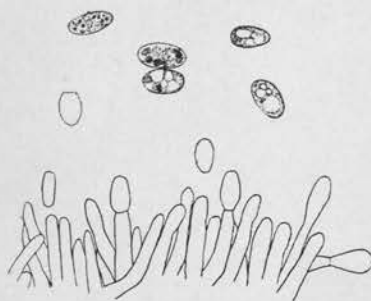


Fig. 2. Conidiophores and conidia of *Phoma citricarpa* McAlpine, $\times 500$.

ERRATA

Page 337, line 32, *for* .05 cubic centimeter *read* 0.5 cubic centimeter.

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[New generic and specific names and new combinations are printed in clarendon; synonyms and names of species incidentally mentioned in the text are printed in *italic*.]

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